Spatial turnover of insect communities at rainforest edges

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Abstract

Rainforest fragmentation is leading to huge increases in the quantity of forest in close proximity to edges. Edge effects may cause multiple alterations to ecological processes, however we do not know their impacts on the spatial turnover of communities, β-diversity. Using a dung beetle community in the north-east Brazilian Amazon, I addressed the problem in four, systematic steps. First, as β-diversity is spatially dependent it is essential to sample at small through to broad scales, presenting us with a limitation of sampling over large areas at fine scales. I present a scalable sampling design based upon a fractal series of equilateral triangles that proved in simulations to be more efficient at recovering accurate estimates of β-diversity than classical sampling designs. Second, I investigated optimal bait choice for accurately sampling the dung beetle community. A human-pig dung mix was found to be as effective as pure human dung baits, whilst removing possible dung source limitations. Third, I investigated the drivers of β-diversity based upon traits that govern foraging strategies. Wing and body morphology was found to be a significant predictor of the spatial scales at which species populations were structured. I then partitioned the variation attributed to environment and space for each morphological subset at three spatial scales. The drivers, and the scales at which they were most important, were dependent upon morphological traits, which further interacted with habitat modification. Finally, I investigated if β-diversity was greater in dung beetles at the forest edge. Linearising the fractal design, I estimated turnover within communities at set distances from the edge. Results were mixed: there was no elevation at a primary-*Eucalyptus* forest edge, but significantly higher turnover within communities at a primary-secondary forest edge than interior communities. This work increases our knowledge of how fragmentation and edge effects impact the underlying processes governing diversity.

Declaration of Authorship

I confirm that the research presented in this document is my own, and that all assistance received has been appropriately acknowledged. Any co-authors of work submitted for publication have been outlined at the start of each chapter. In particular, in Chapter 4 soil granulometric analyses were carried out by Grupo Orsa, and dung beetle morphometric measurements were carried out by Fred Resende Alves at Universidade Federal de Lavras. All other data collection, and all analyses, specimen preparation and identification were carried out by myself.

Signed: **Charlie Marsh**

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Chapter 1

General Introduction

Deforestation of tropical forest continues apace (Millennium Ecosystem Assessment 2005) and habitat loss remains the dominant threat to biodiversity (Gardner et al., 2009, Jetz et al., 2007, Myers et al., 2000). As landscapes are cleared the contiguous habitat is transformed in to progressively smaller patches separated from each other by a matrix of a different habitat, leading to habitat fragmentation (Fischer and Lindenmayer, 2007). The effects of fragmentation on biodiversity are the result of a host of processes, including a reduction in total habitat area (Fahrig, 2003), patch size (Bender et al., 1998), and the isolation of populations in habitat patches (Prugh et al., 2008), as well as the synergistic interactions that may arise between multiple processes (Ewers et al., 2007).

Indeed, so broad a theme is fragmentation that some argue the term has lost meaning and would be better replaced by several key themes (Lindenmayer and Fischer 2007; but see Ewers and Didham 2007). In this thesis, I focus on one such theme, an increase in the proportion of habitat bordering the matrix, which alters a wide suite of ecological patterns and processes that together are broadly termed 'edge effects' (Ries et al., 2004). Edges may include boundaries between patches of habitats ranging from single individuals to regional biomes (Cadenasso et al., 2003), however for the purposes of this thesis I define an edge at a landscape-level as the boundary between two distinct habitat types, one natural and one anthropogenic, as opposed to an ecotone (a natural boundary). More specifically, I will generally consider the effects on the original primary forest communities, although edge effects apply equally to the anthropogenic habitat. I assess the impacts of edges

on patterns of dung beetle diversity, and investigate if spatial turnover, β-diversity, is greater at the edge, and if so, the magnitude and extent of penetration of these impacts.

1.1 The influence of edges on forest communities

Edge effects incorporate a wide range of well-established biotic and abiotic changes (Laurance, 2002, Murcia, 1995) and synergistic interactions between them may result in cumulative impacts on diversity (Laurance et al., 2011, Malcolm, 1994). Ultimately, the influences of edges may be the primary driver of ecosystem responses to fragmentation (Banks-Leite et al., 2010, Ewers et al., 2007).

The underlying cause of ecological changes from edge effects are due to primary processes which affect the structural responses of the forest bordering edges (Harper et al., 2005). These include altered microclimatic fluxes, including light, heat, moisture and wind turbulence (Kapos, 1989, Weathers et al., 2001) and the magnitude and penetration of these changes will depend upon the similarity of the matrix habitat to the original forest habitat (Cadenasso et al., 2003, Matlack, 1994), as well as the age, direction and structure of the edge (Cadenasso et al., 1997, Didham and Lawton, 1999, Kapos, 1989, Matlack, 1993, 1994, Turton and Freiburger, 1997). In forest habitats, this may lead to hotter, drier conditions than the interior (Chen et al., 1999), which combined with an increase in leaf-litter depth and decomposition (Didham and Lawton, 1999) may lead to an increase in surface fire susceptibility (Alencar et al., 2004, Cochrane, 2001). Furthermore the presence of edges increases ease of access to anthropogenic disturbance (Hamberg et al., 2008), increasing rates of agricultural conversion (Morton et al., 2006) and hunting pressure (Peres, 2001).

In turn, these changes cause a multitude of responses to ecological processes at the species and community-level. Primarily, there are changes to the floristic composition and structure of the vegetation close to the edge. Often there is a marked increase in tree mortality near newly-formed edges (Laurance et al., 1998, 1997) that are replaced by fast-growing

successional species (Laurance et al., 2006), resulting in a reduction in shade-tolerant trees due to altered biased seed dispersal (Cramer et al., 2007, De Melo et al., 2006) and germination rates (Bruna, 1999). For vagile organisms, the fragmentation process can lead to a transient hyperabundance of individuals retreating from the lost habitat and crowding into the small remnants that still persist (Hagan et al., 1996), or long term increases in abundance due to increased food availability (Stouffer and Bierregaard, 1995). More insidious changes may arise from long-term changes to the trophic structure of communities due to invasions of edge-tolerant species (Didham et al., 2007, Margules et al., 1994), and changes to the intensity and structure of trophic interactions (Andresen, 2002, Didham et al., 1998b, Steffan-dewenter and Tscharntke, 2002), such as altered predation rates (Hartley and Hunter, 1998, Terborgh et al., 2001) and meso-competitor release (Crooks and Soule, 1999). Many of the ecological processes at forest edges exhibit an increase in the magnitude and frequency of their dynamics, a phenomenon termed hyperdynamism (Laurance, 2002), leading to persistent, increased ecological instability (Wang and Malanson, 2008) and in turn to greater population fluctuations and changes to community composition (Laurance et al., 2011).

Typically, measurable differences in microclimatic variables penetrate only a few hundred metres into the forest interior (Laurance et al., 2002), and the vast majority of studies focus within these distances. However, the impacts on forest species and communities may be much more pervasive (Laurance, 2000). Larger scale investigations have found that species abundances and community-level metrics such as richness, evenness and composition, may be impacted up to a kilometre into the interior (Ewers and Didham, 2008), or even significantly further (Curran et al., 1999).

The rate and spatial configuration of deforestation are causing a rapid increase in the quantity of 'core' habitat being converted to 'edge' habitat (Ewers and Laurance, 2006). For example, by 2002 6.4% of a large proportion of the Brazilian Amazon was within 100 m from the forest edge, and over half within 2 km, with an increase of some 70,000 km of new forest edge per year (Broadbent et al., 2008). Clearly, this represents a significant

quantity of forest under the influence of edges and therefore it is vitally important to determine their effects on rainforest communities and on the ecological processes that shape them beyond the first few hundred metres from the border.

1.2 Estimating variation and turnover between communities

Edge effects are one of the most intensively studied aspects of ecology, yet the majority of these studies focus on the impacts on the abundances or fitness of individual species, or on species richness, α-diversity (Laurance et al., 2002, Ries et al., 2004). Edges may have negative or neutral impacts on diversity, but often we see an increase in species richness at edges where the forest community mixes with the matrix community (e.g. Ewers et al., 2007).

However, the impacts of edge effects are less well established for the spatial component of diversity, β-diversity. β-diversity is at the heart of any investigation that seeks to understand how ecological processes shape patterns of biodiversity and provides us with a direct link between local α-diversity and regional γ-diversity (Anderson et al., 2011, Gering and Crist, 2002, Tuomisto, 2010a). Estimates of β-diversity have been applied to such fundamental questions as the global total (e.g. Stork, 1993) and distribution of species (Qian et al., 2004), predicting extinction rates from habitat loss (Hubbell et al., 2008), species richness relationships (Scheiner et al., 2011) and complementarity of reserve design (Howard et al., 1998, Marsh et al., 2010, Su et al., 2004, Wiersma and Urban, 2005).

However, a bewildering array of metrics exist for estimating the variation in community composition between sites (Gaston et al., 2007, Koleff et al., 2003, Tuomisto, 2010b) and there is little consensus as to which measure is most appropriate to apply to which of the plethora of ecological phenomena termed β-diversity (Anderson et al., 2011, Gaston et al., 2007, Koleff et al., 2003, Tuomisto, 2010a, Vellend, 2001). Moreover, differences in community composition may incorporate simple species identities or include information

on relative abundances (Legendre et al., 2005), phylogenetic variation (Bacaro et al., 2007, Izsak and Price, 2001) or functional diversity (Swenson et al., 2011).

In this thesis I adopt the terminology of Vellend (2001) and Anderson et al. (2011) of 'directional' and 'non-directional' β-diversity, given that they pertain to two different descriptions of diversity patterns: the directional turnover in community composition across a gradient, and the variation of species composition amongst sets of sampling units. The two approaches are not exclusive, however, and it is advisable to use several complementary analyses to better elucidate the variety of ecological processes driving spatial patterns (Anderson et al., 2011). The choices of metrics within these two categories are many, and a hypothesis-driven approach should be used in their selection.

Directional turnover measures the change in community composition between pairs of sites along a directional or environmental gradient. Metrics may model the turnover in species presence, or may additionally incorporate changes in species abundances within the community. Often, the turnover between pairs of sites is regressed against distance to reveal the distance-decay of similarity (Nekola and White, 1999) typical of natural ecosystems (Balvanera et al., 2002, Condit et al., 2002, Hulcr et al., 2008, Jobe, 2008, Morlon et al., 2008, Novotny et al., 2007, Qian et al., 2004, Soininen et al., 2007b), although this relationship is highly spatially-dependent (Soininen et al., 2007b).

Non-directional β-diversity estimates the variability in community composition among sets of samples (Vellend, 2001). A common approach is to additively or multiplicatively partition γ-diversity in to independent α- and β components (Jost, 2007, Lande, 1996, Veech et al., 2002). The β component can be further partitioned into a range of spatial scales (Chandy et al., 2006, Mac Nally et al., 2004, Tylianakis et al., 2006a, Wagner et al., 2000) or temporal timescales (Moreno and Halffter, 2001, Tylianakis et al., 2005). The spatial or temporal turnover in species often comprises a larger proportion of overall diversity, γ-diversity, than local richness (e.g. Crist and Veech, 2006, Gabriel et al., 2006,

Gering et al., 2003) and thus is critical to the processes that define and maintain diversity at all scales. However, partition estimates are strongly dependent on spatial scale, sampling effort and local species richness (Crist and Veech, 2006, Gaston et al., 2007).

There are three principle drivers determining β-diversity. Additive and multiplicative partitioning are closely linked with the first: local-regional relationships and the species area relationship (Crist and Veech, 2006, Gering and Crist, 2002, Loreau, 2000). The two further drivers, niche limitation and dispersal limitation, may be investigated by partitioning the variation in community composition within a set of sites through ordination techniques (Legendre, 2008, Legendre et al., 2005) allowing us to estimate the influence of spatial structure versus environmental variation on patterns of diversity (Borcard et al., 2004, 1992). It has been suggested that these analyses may be used to infer the processes that drive β-diversity (Legendre et al., 2005), with the proportion of variation explained by spatial structure attributed to neutral processes and dispersal limitation, and the variation attributed to environmental drivers explained by niche-based processes (Dray et al., 2012, Legendre, 2008, Legendre et al., 2009). However, any inferences must be made with extreme care (Anderson et al., 2011). For example, there may be unmeasured environmental variables or environmental gradients that are indistinguishable from spatial structures.

Finally, it must always be remembered that measures of β-diversity are spatially dependent, and any measure of β-diversity between two points will depend on the distance between points sampled (Gaston et al., 2007, Gering and Crist, 2002, Loreau, 2000, Nekola and White, 1999, Tylianakis et al., 2006a). It is vitally important to explicitly consider both the sampling grain or resolution (the smallest unit of measurement – α-diversity) and the sampling extent (the furthest distance between all sampling points – γ-diversity) when designing and comparing studies (Wiens, 1989). For example, increasing spatial grain will lead to decreases in β-diversity estimates (Mac Nally et al., 2004), and this decrease will be uneven across measures of turnover (Gaston et al., 2007), levels of disturbance (Dumbrell et al., 2008) and in likelihood between taxa (Hamer and Hill, 2000,

Hill and Hamer, 2004). Indeed I highlight in the second chapter that estimates of β components from partitioning analyses at different spatial scales (non-directional β-diversity) are highly dependent on the sampling effort as well as the configuration of sampling points.

To fully understand the processes driving the responses of communities to fragmentation we need a greater understanding of its impacts on β-diversity and there are several issues that remain unsatisfactorily answered: how is directional turnover affected by increasing habitat modification? Is β-diversity higher at the borders between habitats than in habitat interiors, and how does it change with distance from the edge?

Implicitly, we expect that turnover should increase at the border; as the community in one habitat is replaced by the community in the other (Ewers and Didham, 2008, Spector and Ayzama, 2003). Therefore edges between habitats that share a higher proportion of their communities should exhibit lower turnover than those between highly different habitats. Additionally, ecological processes at forest edges typically show hyperdynamism (Laurance, 2002), exhibiting greater fluctuations and leading to increased ecological instability (Wang and Malanson, 2008) suggesting that turnover should also be higher along the forest edge than in the interior (Ewers and Didham, 2008). However, there is an absence of studies investigating the continuous response of the spatial turnover within communities with distance from the edge, although Duraes et al. (2005) did so across a natural ecotone. In this thesis I seek to estimate changes in β-diversity using dung beetles (Coleoptera: Scarabaeinae) as a target taxon.

1.3 Dung beetles as a focal taxon

Dung beetles have been proposed as an ideal cost-effective target taxon for investigating patterns of diversity (Gardner et al., 2008a, Gardner and Nichols, 2011, McGeoch et al., 2002, Spector, 2006), and unusually for an invertebrate taxon in the tropics are well established taxonomically for the study area (Gardner et al., 2008b). They also, fulfil

several important roles in the rainforest ecosystem, including secondary seed dispersal, soil perturbation, parasite suppression and nutrient cycling (Andresen, 2002, Nichols et al., 2008).

Dung beetles generally ascribe to three nesting strategies that have consequences for their ecological functioning (Doube, 1990, Vulinec, 2002). Parocoprid species tunnel underneath the dung deposition, endocoprids brood young directly within the dung deposition, and telocoprids roll dung balls a distance away from the dung deposition (Halffter and Matthews, 1966). The brooding strategy, along with body size, are strong determinants of the efficiency of dung removal and consequently seed dispersal (Slade et al., 2007). Larger beetles bury more seeds, of larger sizes, and to greater depths (Andresen, 2002). Burial depth is an important determinant of seed fate, as shallow seeds are more susceptible to rodent predation (Estrada and Coates-estrada, 1991), although seeds that are buried too deep, however, have decreased germination rates (Shepherd and Chapman, 1998). In general, however, seeds buried by beetles have higher germination rates (Andresen, 2003).

The responses of dung beetles to habitat disturbance are well understood, as well as the important consequences this may have for ecosystem functioning. Dung beetle communities are known to be highly sensitive to habitat disturbance (Arellano et al., 2005, Davis et al., 2001, Gardner et al., 2008b, Kessler et al., 2009, Nichols et al., 2007, Scheffler, 2005, Shahabuddin et al., 2010, 2005, Vulinec et al., 2006) and fragmentation (Andresen, 2003, Feer and Hingrat, 2005, Filgueiras et al., 2011, Klein, 1989, Larsen et al., 2008), with communities becoming more dissimilar to primary forest communities with increasing disturbance (Davis et al., 2001, Davis and Philips, 2009, Nichols et al., 2007, Scheffler, 2005, Shahabuddin et al., 2010). Losses in dung beetle richness, abundance or functional diversity may result in a decrease in functionality such as lower rates of dung and seed removal (Andresen, 2003, Klein, 1989, Shahabuddin et al., 2010, Slade et al., 2011, 2007, Yamada et al., 2007), resulting in a concomitant decrease in plant productivity (Wu et al., 2011). Larger bodied species are more susceptible to disturbance and fragmentation (Andresen, 2003, Clough et al., 2007, Filgueiras et al., 2011, Gardner et al., 2008b, Klein,

1989, Larsen et al., 2008, Scheffler, 2005) but have a disproportionate contribution to ecosystem functioning (Larsen et al., 2005). The loss of large paracoprids may reduce dung removal rates by 75%, although there is high complementarity between functional groups (Slade et al., 2007). They can also be highly sensitive to edges, and there may even be an almost complete turnover in community composition across ecotones (Spector and Ayzama, 2003), although responses may be mixed (Duraes et al., 2005, Feer, 2008).

1.4 Outline of studies

In this thesis I address some of the shortcomings in the current literature. I aim to assess whether β-diversity is elevated at rainforest edges in dung beetle communities, and attempt to quantify the strength and penetration of any such elevations across several boundary types. I approach the subject systematically in four stages.

First, I address issues in accurately estimating β-diversity using standard sampling designs. As β-diversity is a spatially-dependent process, species turnover must be estimated at the small, local scales at which species interact right through to the large, landscape-level scales at which population dynamics operate, and moreover that estimate needs to be equally accurate across all spatial scales (Kraft et al., 2011, Tylianakis et al., 2006a). However, when resources are limited we must compromise between the need to collect fine-scale data and the ability to cover broad-scale distances. The self-similarity of fractals presents us with a suitable framework for developing such a sampling design and that is the subject of Chapter 2.

Second, any estimate of β-diversity is dependent upon accurately describing community composition at our sampling grain, α-diversity. In Chapter 3 I identify an optimal sampling strategy for sampling dung beetle communities by assessing dung preference.

Third, I investigate the drivers and spatial scales important in determining species turnover, and if these spatial scales can be linked to functional traits. Morphometric traits of body

and wing characteristics may determine the flight ability and foraging strategy of dung beetles. In Chapter 4 I identify the spatial scales determining species distributions and link them to morphometric traits that govern foraging distances. I then apply variation partitioning to determine the drivers of β-diversity at multiple spatial scales for separate foraging categories.

Finally, in Chapter 5, I estimate levels of community turnover at rainforest edges. By applying our fractal-based sampling design I was able to estimate β-diversity within edge communities and compare those levels against communities in habitat interiors and at various distances from the edge.

Chapter 2

A fractal-based sampling design for ecological surveys quantifying β-diversity

Charles J. Marsh & Robert M. Ewers

Accepted for publication in Methods in Ecology and Evolution. Figures have been reformatted to fit the thesis layout

2.1 Summary

1. Species turnover, β-diversity, underpins a number of ecological processes that define patterns of diversity. Estimates of β-diversity are dependent upon the spatial scale investigated, and patterns may vary across spatial scales. This presents us with a logistical problem of how to sample sufficiently at fine, local-scales through to broad, landscape-scales in order to provide accurate estimates of β-diversity at all spatial scales.

2. Here, we present a scalable sampling design based on fractal geometry that is designed to explicitly address questions about β-diversity. Using simulated communities we assessed the efficacy of the fractal design, along with two further designs representing subsamples of the fractal design and several classical ecological sampling designs (grids and transects) to estimate β-diversity across multiple spatial scales using two measures of β-diversity: community dissimilarity modelled against geographic distance, and additive partitioning.

3. All designs successfully modelled dissimilarity against distance, with the exception of grid sets and transects that were found to be unsuitable. When diversity was partitioned into multiple spatial scales, all sampling designs overestimated large-scale β-diversity.

4. The accuracy of distance-decay estimates were primarily determined by the spatial configuration of sampling points. By contrast, the accuracy of diversity partitioning estimates was also influenced by sampling effort, with insufficient sampling effort and unsuitable sampling point configuration causing overestimates of β-diversity at larger spatial scales. We recommend that studies investigating β-diversity use a cluster-based configuration of sampling points, such as the fractal-based design presented here, in order to ensure accurate and comparable estimates at multiple spatial scales. Furthermore, when comparing results between studies, care should be taken to account for differences in sampling grain, sampling effort and the configuration of sampling points.

2.2 Introduction

Identifying patterns of diversity are crucial to our understanding of the maintenance of ecosystems and the mechanisms of the ecological processes that shape them. Many studies estimate diversity at local scales for comparisons between habitats, across natural and non-natural habitat modifications, as well as ecological, latitudinal and elevational gradients. However, fewer studies investigate the spatial component of diversity, β-diversity, although this component may be equally as effected by such processes.

Species turnover underpins numerous ecological processes and rigorous estimates of β-diversity are crucial in our investigation of these fundamental phenomena across a range of spatial scales (Anderson et al., 2011). Examples include assessing the complementarity of species in reserve networks (Marsh et al., 2010, Su et al., 2004, Wiersma and Urban, 2005), right through to making predictions of global species richness (Ødegaard, 2000), as well as processes that require estimates at multiple spatial scales, such as the distributions of species (Qian et al., 2004) and extinction rates from habitat loss (Hubbell et al., 2008).

Investigations that have partitioned diversity into α, β, and γ components (Lande, 1996) have found that the β component may comprise of a significant portion of overall richness, γ-diversity, often much greater than that of local richness (e.g. Gering et al., 2003). This important component of diversity may be further partitioned temporally (Tylianakis et al., 2005), across multiple spatial scales (Crist et al., 2003, Veech et al., 2002, Wagner et al., 2000)

Only rarely, however, are studies explicitly designed to quantify β-diversity, and data are rarely collected in the field with analyses of community turnover as the primary focus. Given the importance of β-diversity to a plethora of ecological and conservation issues, we suggest there is a need to develop a spatial sampling strategy designed explicitly to estimate β-diversity over a range of spatial scales. We approach this problem by designing a range of possible sampling strategies based around fractals, and use simulations

of tropical communities to investigate the optimal sampling strategy that compromises between the accuracy of β-diversity estimates and sampling effort.

Fractal mathematics (Mandlebrot, 1983) has become increasingly popular to describe a wide range of ecological processes in which Euclidean geometry has proven insufficient. For example, many ecological processes are spatially dependent, and the self-similarity of fractals can infer such patterns by scaling-up or down spatial scales based on observations made at a particular scale. Fractal geometry has been applied to a diverse range of topics in ecology and conservation biology (Brown et al., 2002, Halley et al., 2004). For example, species aggregations are often self-similar across a range of spatial scales (Kunin, 1998), so fractals provide a useful model for understanding the spatial distributions of species (Storch et al., 2008, Ulrich and Buszko, 2003) and several associated macroecological patterns, such as species-area relationships (Lennon et al., 2002, Sizling and Storch, 2004, Tjørve and Tjørve, 2008).

However, fractal geometry has been used surprising rarely to investigate the spatial turnover of species, β-diversity. Early models of species coexistence on fractal landscapes suggested that β-diversity may be a function of the fractal dimension of a landscape (Palmer, 1992), and there is some evidence that β-diversity of plants across Britain may be described fractally (Kunin, 1997). Only a single study has considered using fractals as a basis to collect data when studying these processes. Kallimanis et al. (2002) found that a sampling design based upon a fractal network of rectangles, Cantor grids (Mandlebrot, 1983), was more successful in measuring the fractal dimension of a species distribution than classical line transects, but no study has built on this result to investigate optimal sampling strategies to quantify species turnover. Here we explore several possible fractal-based sampling designs for estimating β-diversity.

2.2.1 Criteria for a sampling design

Any sampling design for investigating β-diversity should incorporate two main criteria. First, any measure of β-diversity between two points will depend on the distance between points sampled, i.e. β-diversity is dependent on the spatial scale at which it is measured (Gaston et al., 2007). Therefore, any sampling design should cover a range of spatial scales, from the fine scales at which individuals interact (Huston, 1999), through to broad, landscape scales at which population dynamic processes occur (Gering and Crist, 2002). Second, following the principle that the variance can be more important than the mean (Benedetti-Cecchi, 2003, Halley et al., 2004) it is vital that any estimate of β-diversity is accompanied by a measure of variance around that estimate.

The need to obtain fine-scale (grain) data over large spatial scales (extent) immediately poses logistical limitations. For studies utilising remotely-sensed or pre-existing data, fine-scale data can be seamlessly aggregated up to large spatial scales at almost no additional expense other than processing power (e.g. Kunin, 1998). However, for field-based studies, frequently limited by logistical constraints, trade-offs between sampling effort and statistical power are inevitable. Using classical ecological sampling designs, such as regular grids, every order of magnitude increase in spatial scale can require a 10 or 100-fold increase in sampling effort (Halley et al., 2004, Kallimanis et al., 2002), which quickly becomes unfeasible and forces us to focus our sampling on a subset of spatial scales.

A fractal-based sampling design, based around clusters of sampling points rather than the regular or random placement of sampling points, could allow us to overcome these limitations, scaling up to larger landscape levels with a significantly smaller increase in sampling effort than using a regular grid. As fractal patterns are self-similar across a range of spatial scales, a design such as Cantor grids allows for an efficient method of sampling fine-scale processes while simultaneously sampling large-scale processes with the same design Kallimanis et al. (2002). Furthermore, a fractal-based sampling design

ensures that we can generate multiple estimates of the response variable(s) at each spatial scale investigated, as well as a measure of the variance around those estimates.

Cantor grids require four points to define a rectangle. However, only a minimum of three points are necessary in order to obtain a mean of β-diversity estimates (i.e. three is the minimum number of points required to obtain more than one point-to-point comparison of species identities), although there will be a subsequent decrease in the accuracy of the estimate of the mean and variance. If we wish to increase accuracy we could increase the number of points to five (pentagons), six (hexagons) or more. However, this gain in precision must be counterbalanced by the increase in sampling effort at a given spatial scale.

This leads to a fractal pattern based on equilateral triangles being an efficient method of sampling across multiple spatial scales while keeping sampling effort to a minimum (Fig. 2.1a), although with the drawback that it also equates to the fractal based pattern that is likely to have the highest error (largest confidence intervals) in parameter estimates. To generate the triangle fractal design, we arrange three sampling points on the vertices of an equilateral triangle with sides of length 10^w, where w is a scaling factor. The scaling factor will necessarily vary according to the taxa being investigated, with studies on large, vagile taxa requiring a larger scaling factor than smaller, sedentary taxa. This distance defines the value of w, and allows the mean and variance of β-diversity to be estimated over distance 10^w, which represents the '1^{st}-order' of the spatial scales at which sampling is being conducted.

A full sampling scheme will extend across N orders, with the 2^{nd}-order samples being separated by distances of 10^{2w} and so on. However, the 2^{nd}-order samples are not represented by a single point, but rather by a 1^{st}-order triangle centred on that point, requiring nine points to simultaneously sample at the 1^{st} and 2^{nd}-order spatial scales. The number of sampling points (S) in the full sampling design, then, increases exponentially with the number of spatial scales (N) according to the function $S = 3N$. Further increases in spatial

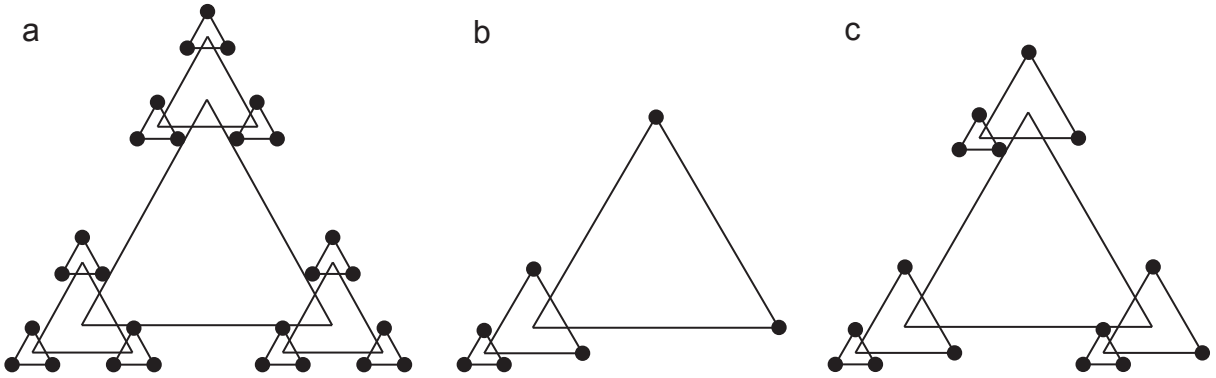


Figure 2.1. Fractal sampling designs based on equilateral triangles and extending across three spatial scales ('orders'). The sampling points (black dots) are located on the apices of each 1st-order triangle. Three designs are presented: (a) the full fractal design; (b) a subsampling strategy using the minimum number of points to obtain β-diversity estimates at all spatial scales; and (c) the compromise subsampling strategy that attempts to balance sampling effort and statistical power.

scale are added by siting the lower order sampling pattern on the apices of higher order triangles along progressively larger scales (10^{3w}, $10^{4w} \ldots 10^{Nw}$).

2.2.2 Trade-offs between sample size and cross-scale information

Because the number of sample points increases exponentially as we add additional spatial scales, where resources are limited it may become logistically infeasible to employ the full fractal design across numerous spatial scales. However, the self-repeating nature of a fractal design allows for field studies to subsample in ways that reduce the sampling effort required while retaining β-diversity estimates, and variance around those estimates, at all spatial scales.

To reduce sampling effort to the minimum, we can replace two out of every three clusters of points with a single sample point located within the centre of the cluster it replaces (Fig. 2.1b). This retains the ability to obtain a mean and variance estimate of β-diversity at each spatial scale, although with a reduction to just a single estimate for each scale whereas in the full fractal design the number of estimates increases with decreasing scale. In this situation, the minimum sampling effort required ($S_{\min}$) scales linearly, rather than exponentially, with the number of spatial scales, with $S_{\min} = 2N + 1$. This, then, allows

for a much larger range of spatial scales to be investigated with relatively small additional investments in sampling effort.

Finally, we present a third sampling design that attempts to balance the number of sampling points with the number of β-diversity estimates at lower orders of spatial scale (Fig. 2.1c). This design maintains one full triangle of sampling points at the apex of each 2$^{\text{nd}}$-order triangle, which is repeated at each apex of the 3$^{\text{rd}}$-order triangle and so on. While still significantly reducing the number of sampling points, there are now a number of β-diversity estimates at lower order spatial scales. Therefore we may consider this as a compromise (S_{com}) between sampling effort and statistical power. In this case $S_{\text{com}} = 5 \times 3^{N-2}$, where $N \geq 2$. While sampling effort here also scales exponentially with the number of spatial scales, it still approximately halves the number of sampling points needed relative to that of the full fractal design.

2.3 Materials and Methods

We used simulations to compare the ability of various sampling designs to accurately estimate β-diversity across spatial scales. We generated communities across a 'landscape' (R code can be found in Appendix A.1) in which we independently tested a range of sampling designs. By controlling species richness and β-diversity we were able to separate the relative importance of sampling effort and the configuration of sampling points on generating estimates of β-diversity across multiple spatial scales. All simulations were created and analysed in program R version 2.13.1 (R Development Core Team 2011).

2.3.1 Creating a simulated community

To provide an 'ecological space', we created a hypothetical landscape consisting of a 100×100 cell grid, overlaid with a single, linear environmental gradient ranging from -1 to 1 oriented in a random direction. By increasing the range of gradient values, species distribution patterns become more polarised in space and thus β-diversity can be generated in our hypothetical landscape. By randomising the gradient direction we can

investigate the differences in accuracy between sampling designs that are unidirectional (e.g. transects) compared to multidirectional (e.g. regular grids) in situations where we do not know *a priori* the direction of the gradient(s) driving patterns of β-diversity.

To distribute species across the landscape in patterns that emulate those found in natural ecological communities, we randomly assigned each of i species a value for three parameters: a probability of occurrence (ψ_i), a degree of density dependency (d_i), and a response to the environmental gradient (e_i). This approach provides the flexibility to alter the probability distributions of each parameter to match those found in real communities. In our study, we generated communities resembling a tropical insect community. Values for ψ were taken from a left skewed beta distribution that corresponds to a community of mostly rare species and few common species. Values of d recorded the strength of density dependence, and were used only if the species was present in a neighbouring cell. Values were selected from between -0.5 and 0.5 sampled from a normal distribution, so that approximately half the species were negatively density dependent with some degree of scattering and half were positively density dependent and exhibited aggregated distributions. Similarly, the values for e were also taken from a normal distribution between -0.5 to 0.5, so that approximately half the species were more abundant on one side of the gradient and the other half were more abundant at the opposite end. Species with a value of $e = 0$ were insensitive to the gradient. Species were populated independently of others, such that multiple species could occupy a cell without influencing the occupation of other species.

We combined these values to determine the value ($P_{i,k}$) that species i will be present in a given cell k according to the equation

$$P_{i,k} = \psi_i + (d_i \times D_{i,k}) + (e_i \times E_k), \tag{2.1}$$

where $D_{i,k}$ represents the presence ($D = 1$) or absence ($D = 0$) of species i in a cell adjacent to cell k, and E_k represents the value of the environmental gradient in cell k.

To convert these values into a presence-absence matrix we generated a random number between 0 and 1 from a uniform distribution for each of the k cells (R_k) to mimic the natural stochastic element in species distributions (species may be absent even if the environmental conditions are suitable for it to be present). The presence or absence of species i in cell k was determined using the rule

$$\begin{aligned} if: R_k \leq P_{i,k} \qquad then: \quad & P'_{i,k} = 1 \\ else: \quad & P'_{i,k} = 0, \end{aligned} \tag{2.2}$$

where $P'_{i,k}$ is the presence (1) or absence (0) of species i in cell k.

When the landscape is first populated in this manner, a given cell will not be surrounded by eight cells that have had presence-absence determined and so calculations of density dependency will be inconsistent across the landscape. Therefore, we first populated

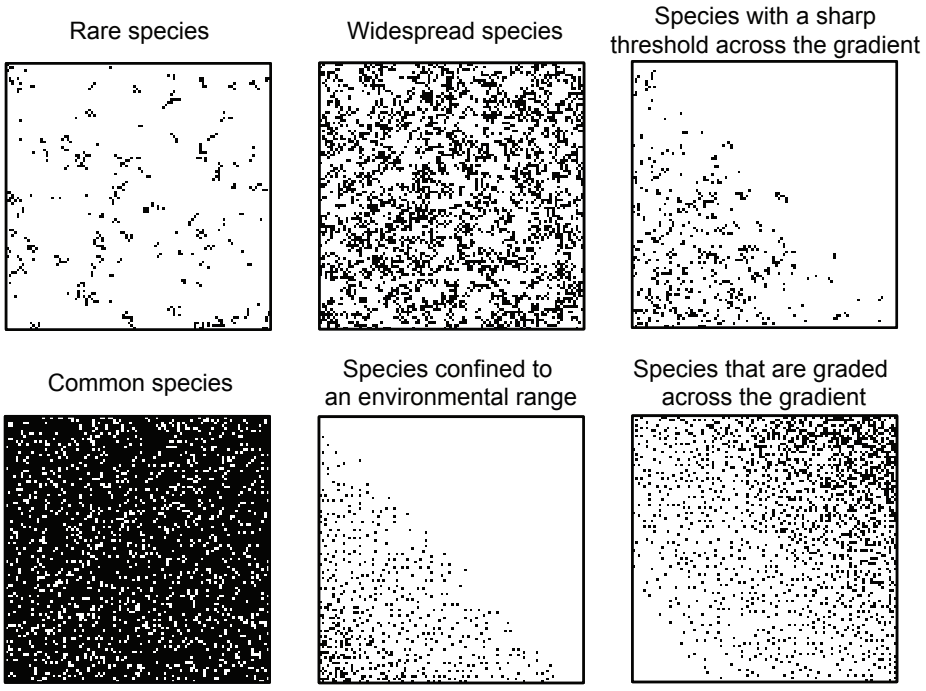


Figure 2.2. Six examples of possible species distributions (presence = black cells) that could be generated using the simulation procedure outlined in the Methods. In the simulated communities created for the analyses approximately half the species will show distributions with some degree of aggregation and half some degree of scattering.

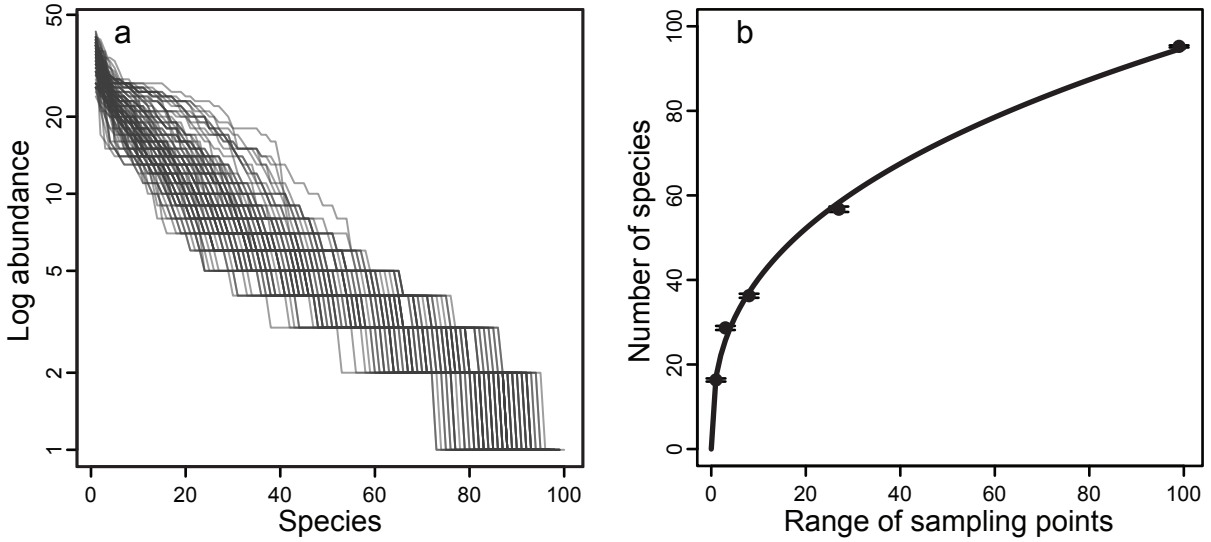


Figure 2.3. Characteristics of simulated communities using the method outlined that approximate those in real tropical communities. Plots are taken from 100 communities sampled by the compromise triangle fractal. (a) rank abundance curves for each of 100 runs, and (b) species-area relationship of mean species richness ± se (non-linear regression: $z = 0.19$, $p < 0.001$)

the landscape in a random order, then repeated the process in a second iteration that produced the final presence-absence matrix for each species. This approach produced a range of realistic species distributions (Fig. 2.2 provides examples of some possible distributions generated with the procedure). We generated landscapes with communities of $i = 100$ species that had similar characteristics of community structure and species area relationships as natural tropical communities (Fig. 2.3)

2.3.2 Sampling designs

We tested seven sampling designs for their ability to estimate β-diversity by comparing them against a control design consisting of 1089 points arranged in a fine-scale regular grid with two cells separating each sample point (Fig. 2.4). First, we explored the three variations of the triangle fractal design described above (Fig. 2.1): (i) a full fractal design extending across four orders of scale; (ii) the compromise subsampling scheme for a triangle fractal design; and (iii) the minimum number of points necessary to subsample the triangle fractal design. As the second design is taken as a compromise between sampling effort and statistical power, all subsequent designs were designed to have equivalent

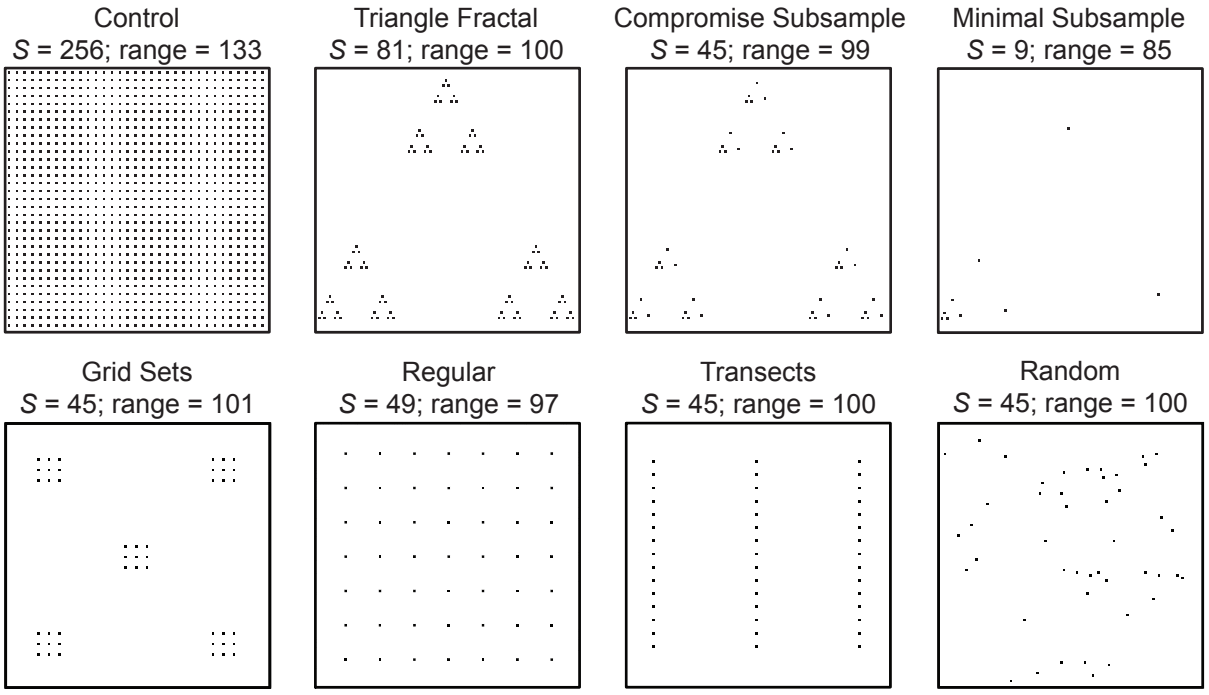


Figure 2.4. Seven sampling designs used to recover patterns of β-diversity. Black points represent the location of a sampling point. Subtitles indicate the name of the sampling design, the number of sampling points, *S*, and the range of distances that separate individual sampling points.

or nearly equivalent sampling effort, and to have a similar range of distances between sampling points. A fourth sampling design (iv) was composed of five sets of grids that might represent a study investigating, for example, within- and between-plot turnover (Tylianakis et al., 2006b). Two further designs, a regular grid (v) and line transects (vi), are frequently used in ecological investigations and so were also tested in these simulations. Finally we included a random sampling design (vii), in which sampling points were randomly distributed across the landscape.

The potential robustness of each sampling design to an environmental gradient of unknown direction was visualised by creating a heat map of distances between sampling points and the bearing between those points. A poor design will have large areas of 'cartesian space' without sampling points, and so would likely produce inaccurate estimates of β-diversity if the direction of the gradient happened to fall within these bearings.

However, if the gradient is the same direction as the bearing between many points (e.g. directly along a transect) highly accurate estimate should be produced.

2.4 Analyses

For each sampling design we distributed 100 species across the landscape. The process was repeated for 100 landscapes for each design and β-diversity estimated within each. To compare the ability of a sampling design to quantify β-diversity, we determined the range of spatial scales over which β-diversity can be estimated for each design and the accuracy of those estimates at different spatial scales. To achieve this, two types of β-diversity were estimated, directional turnover and non-directional variation (Anderson et al., 2011).

Directional turnover was calculated as Bray-Curtis dissimilarity between all pairs of points. Dissimilarity was modelled as a function of distance between points and plotted using the 'loess' function in R, a non-parametric technique of fitting a smooth line from a local regression model. The degree of variance among iterations of the sampling simulation represents the likelihood of a sampling design estimating β-diversity accurately. Using the control sampling design, we generated a 90% confidence interval representing uncertainty in the 'true' estimate of dissimilarity among points separated by a given distance. Similarly, we generated a 90% confidence interval around dissimilarity estimates for each sampling design which we then compared to the control confidence interval. Sampling designs with confidence intervals that match those of the control were considered to give accurate estimates of β-diversity.

To estimate non-directional variation, we hierarchically partitioned diversity into multiple additive components (Lande, 1996). Diversity was estimated at four spatial scales, calculated using moving windows of sizes (i) 1×1, (ii) 5×5, (iii) 15×15, and (iv) 29×29 cells. For a given spatial scale, N, α-diversity at that scale, α_N, was the mean number of species recorded in every moving window. For the regular grid, line transects and random

designs which are not *a priori* designed for partitioning diversity, sampling points could be included in more than one moving window. There is, however, no such pseudoreplication in the fractal designs. By taking total diversity, γ, as the total number of species recorded from all sampling points, for our largest spatial scale ($N = 4$ and a window of 29×29 cells), we calculated β-diversity as $\beta_4 = \gamma - \alpha_3$, and for decreasing spatial scales as $\beta_N = \gamma - \alpha_{N-1}$. Repeated on the 100 simulated landscapes, this returned mean (and variance) estimates of α, β_1 through to β_4, and γ for each sampling design. To quantify the ability of each design to recover known patterns of diversity, we plotted all diversity estimates against those generated from the control design. Best fit lines were generated from linear models with polynomial functions. For each sampling design we used Tukey's honest significant difference tests to determine if the mean estimate for diversity at each spatial scale was significantly different from that estimated from the control design.

2.5 Results

Heat maps of the distances between sampling points highlighted large differences in the configurations between sampling designs (Fig. 2.5). Random and regular designs had the most consistent coverage although the latter had no estimates of β-diversity at very local scales. The fractal designs had consistent coverage across all distances, although the minimal subsampling design was unsurprisingly sparse given the extremely small number of sampling points. Transects had very little coverage at small scales and grid sets produced an uneven distribution.

All sampling designs that we tested produced similar dissimilarity-distance slopes when averaged over the 100 runs (Fig. 2.6). However, there were considerable differences in the range of distances over which each sampling design was able to estimate dissimilarity, and the between-run variance in those estimates. Unsurprisingly, given the very limited sampling effort, the minimal subsampling design had the highest variance, and therefore the least accurate β-diversity estimates (Fig. 2.7). The other two triangle fractal designs tended to slightly underestimate β-diversity at all distances, but produced slopes similar

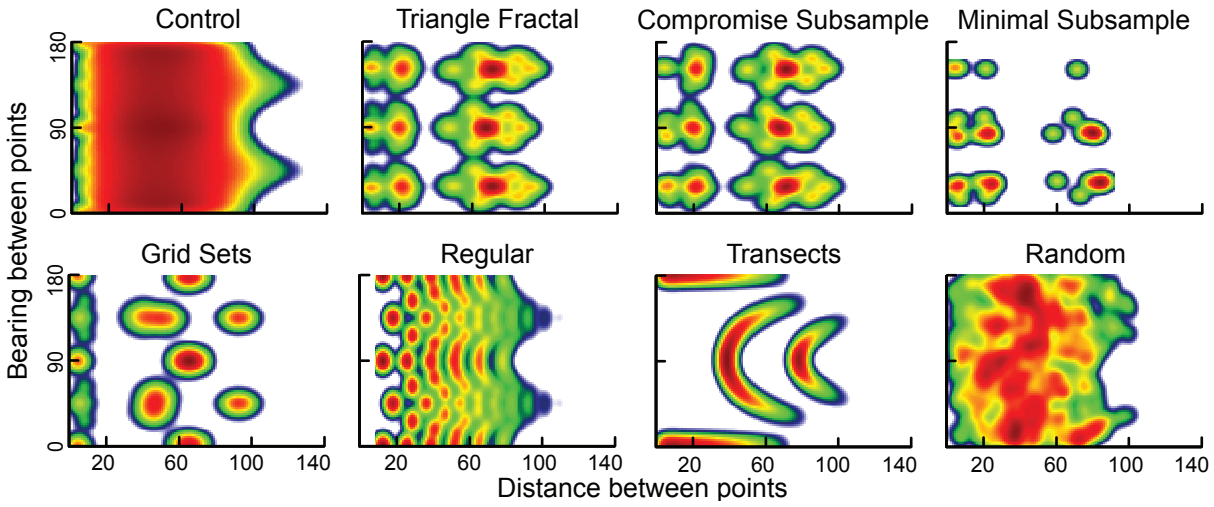


Figure 2.5. Heat maps showing the distances between points against the bearings between points for each sampling design. Values are shown on a colour scale extending from white (indicating no pairwise comparisons) to dark red (the most pairwise comparisons). Designs that minimise the quantity of white areas will be more accurate at estimating β-diversity in situations where we do not know *a priori* the direction of environmental gradient(s) driving spatial turnover.

to that of the control. Of the classical designs, the regular grid provided the most accurate estimates across all distances, but was unable to generate estimates at very small scales. The random design consistently overestimated β-diversity. The final two designs, grid sets and transects provided variable estimates, with dissimilarity-distance slopes that varied depending on the range of distances being examined. Grid sets underestimated or overestimated β-diversity at different spatial scales, whereas transects were accurate at small scales but produced highly variable estimates at medium or large distances.

Estimates of γ-diversity were predictably associated with sampling effort. Sampling designs with 45 sampling points recorded around 95% of all species present (Fig. 2.8a). The full fractal design, with almost twice the sampling effort, recorded 98% of species, whereas the seven points of the minimal subsampling design recorded on average only 55% of all species. The proportion of diversity attributable to local richness (α-diversity) was even across designs (15–17%), except for the minimal subsampling design where α composed 28% of diversity. The classical designs of regular grids, transects or random sampling were unsuitable for partitioning diversity and were not able to partition diversity at the

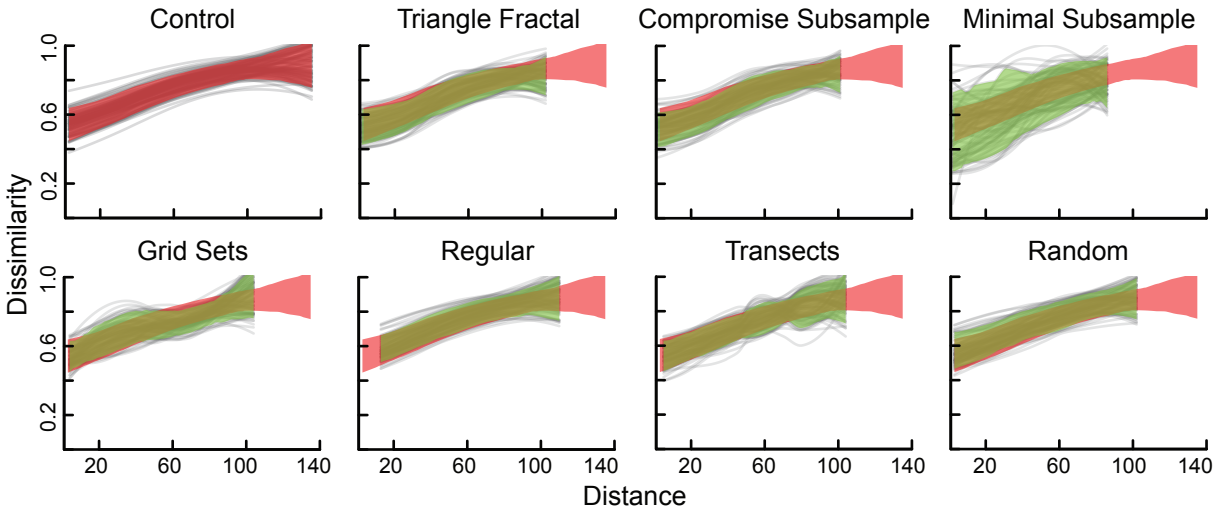


Figure 2.6. Bray-Curtis dissimilarity against distance between sampling points. Light grey lines represent loess functions fitted to the data generated from 100 simulation runs. Here, we present as polygons the region delimited by the inner 90 lines for each sampling design (90% confidence interval; green polygons), and compare them to the 90% confidence interval generated by the control sampling design (red polygons).

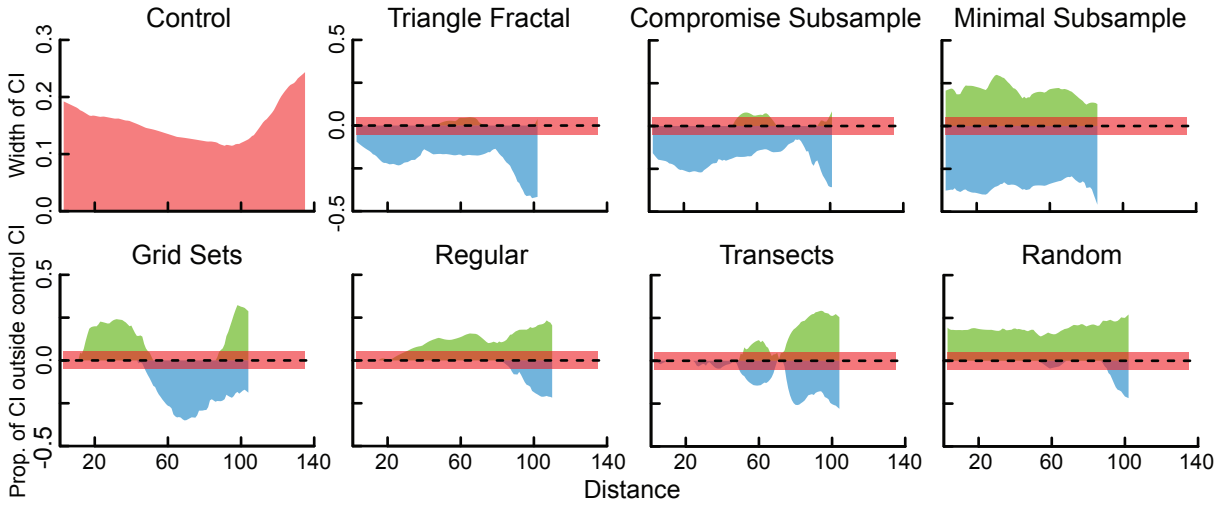


Figure 2.7. The proportion of the confidence interval for each sampling design that falls outside the confidence interval of the control design. The control subplot (top left) indicates the width of the 90% confidence interval surrounding β-diversity estimates for the control (from Fig. 2.5), with lower values representing more accurate estimates. For all other sampling designs, polygons represent the proportion of the 90% confidence interval surrounding β-diversity estimates at a given distance that were greater than (positive values, green polygons) or less than (negative values, blue polygons) the confidence interval determined in the control. Polygons that fall within the red shaded area indicate distances at which <5% of the confidence interval was outside the confidence interval of the control.

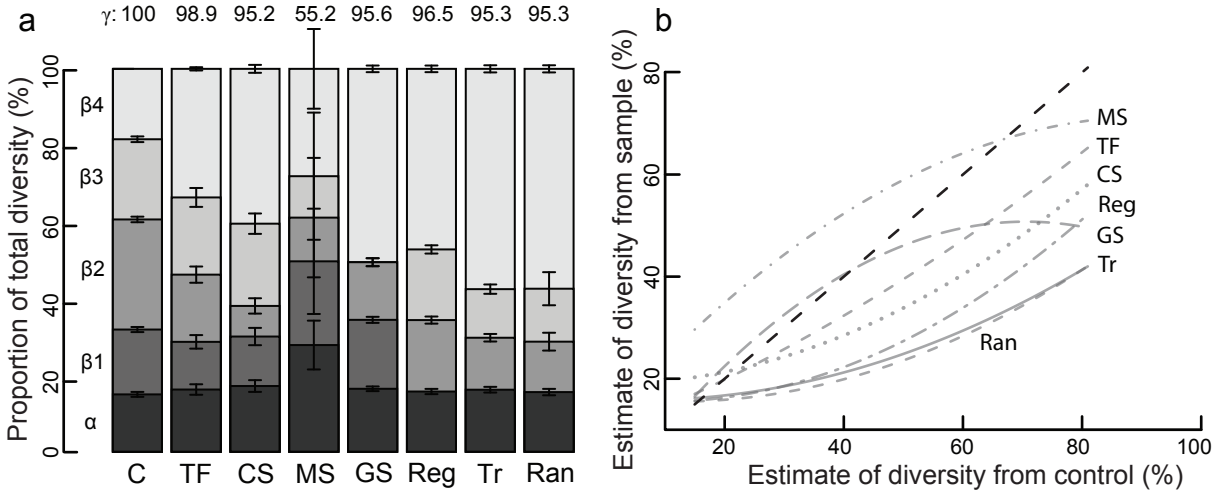


Figure 2.8. (a) Additive partitioning of diversity into five components of increasing spatial scale: α-diversity (very dark grey); β_1 (dark grey); β_2 (grey); β_3 (light grey); and β_4 (very light grey). Estimates of γ-diversity are presented above each sampling design. Error bars are 95% confidence intervals for the diversity estimate at each spatial scale. (b) The estimates for the seven sampling designs were plotted against the partitioned diversity estimates from the control sampling design. Lines of best fit were obtained from a polynomial linear model. The dotted black line represents the 1:1, which would reflect a sampling design that partitioned diversity exactly in accordance with the control. Fitted lines above the 1:1 line underestimate β-diversity, while those below overestimate -diversity. Sampling designs are C = control; TF = triangle fractal; CS = compromise subsample; MS = minimal subsample; GS = grid sets; Reg = regular; Tr = transects; and Ran = random.

smallest spatial scales (Table 2.1). The fractal and grid sets designs produced β estimates more similar to the control than the other designs, although only the fractal designs were able to partition β-diversity across all four spatial scales. However, all sampling designs significantly overestimated the proportion of β-diversity at the largest spatial scales (Fig. 2.8b).

2.6 Discussion

Due to limited time and resources there will necessarily be a trade-off between collecting data able to accurately detect spatial patterns at fine *versus* broad-scales. An appropriate sampling design should attempt to allow researchers to estimate β-diversity at a range of spatial scales, and with a similar level of accuracy at all scales using a variety of complementary methods (Gaston et al., 2007). No sampling design produced estimates with the same accuracy as the control but there were clear differences between the performances

Table 2.1. Relative performances to the control of each sampling design in estimating dissimilarity against distance and partitioning diversity across multiple spatial scales. (a) Comparison of directional dissimilarity estimates between sampling designs and the control design at small (distance = 5), medium (distance = 50) and large (distance = 95) scales. Values represent scales at which >5% of the dissimilarity-distance estimates fell above (+) or below (−) the confidence limits of dissimilarity estimates generated by the control design. Tick marks (✓) indicate scales at which >95% of estimates fell within the control estimates, and NA represents scales at which dissimilarities could not be calculated by a sampling design. (b) Significant differences between the additive diversity partitions estimated for each sampling design and those estimated from the control design across four spatial scales. Symbols indicate if the estimate of diversity was greater than (+), less than (−), or did not differ significantly (✓) from the estimate from the control. NA represents diversity partitions that could not be calculated by a sampling design.

	(a) Dissimilarity-distance			(b) Diversity partitioning				
Sampling design	Small	Medium	Large	α	β_1	β_2	β_3	β_4
Triangle Fractal	−	−	−	✓	−	−	✓	+
Compromise subsample	−	−	−	+	−	−	✓	+
Minimal subsample	+/−	+/−	NA	+	✓	−	-	+
Grid sets	✓	−	+/−	✓	✓	−	NA	+
Regular	NA	+	+/−	✓	NA	−	−	+
Transects	✓	−	+/−	✓	NA	−	−	+
Triangle Fractal	+	+	+/−	✓	NA	−	−	+

of each design (Table 2.1), highlighting that when sampling effort is consistent the configuration of sampling points may have large impacts on our estimates of β-diversity at different spatial scales.

2.6.1 Towards an optimal sampling design to investigate turnover

When estimating directional turnover, there was a clear distinction between designs that produced consistent slopes of the dissimilarity-distance curve across all spatial scales in a manner equivalent to the control, and designs such as grid sets and transect designs that produced variable slope estimates (Fig. 2.5). The minimal subsample design also falls in to this category, although this is unsurprising given the extremely small number of sampling points. The explanation for the relatively high variability returned by these designs is that they have the greatest amount of 'Cartesian space' unoccupied by pairwise comparisons of points (Fig. 2.5). Consequently, these designs have very high uncertainty in β-diversity estimates when the direction of an environmental gradient does not correspond with the

'direction' of the sampling design. Of the other designs, the regular grid provided the most consistent estimates (Fig. 2.7) but has the limitation that if the same range of spatial scales is to be covered as other designs it becomes impossible to also sample at the smallest spatial scales. The random design and the fractal designs also performed well, although they overestimated and underestimated β-diversity respectively.

All designs were inferior at partitioning diversity than at estimating dissimilarity-distance patterns. Grid sets produced the most accurate diversity partitioning estimates, although the fractal designs were the only designs that were able to partition diversity across all four spatial scales (Fig. 2.8). All designs produced diversity estimates at large spatial scales that were significantly lower than the control (Table 2.1). Sampling effort is important in any estimate of an ecological process (Kallimanis et al., 2002) and it is apparent from the relative performances of the compromise subsample, full fractal and control designs that a reduction in the quantity of sampling points results in an increase in large-scale β-diversity estimates. There is, however, an important role played by the spatial configuration of sampling points when sampling effort is kept constant. In particular, sampling designs that are not cluster based appear unsuitable for partitioning diversity across multiple spatial scales, and are also likely to attribute a greater proportion of diversity to large scales than is actually the case.

Across all the designs we considered, we suggest that the fractal design represents the most parsimonious design to capture relatively accurate estimates for both dissimilarity-distance and diversity partitions across all spatial scales. Furthermore, the similarity in performance of the optimal subsampling scheme to the full fractal design suggests that sampling effort can be reduced to a minimum level with only negligible decreases in the accuracy of β-diversity estimates, representing a considerable advantage for data collection in the field. Our results do, however, illustrate the difficulty in defining a single sampling design that can be confidently relied upon to accurately estimate different forms of β-diversity. For example, a design based upon grid sets appears accurate in partitioning diversity but not for estimating directional turnover. By contrast, the regular grid and

random designs estimate turnover accurately but are unsuitable for diversity partitioning as well as being unable to produce fine-scale β-diversity estimates and being impractical to implement in the field respectively. The most commonly employed classical design, transects, performed poorly in recovering both measures of β-diversity.

2.6.2 Limitations of quantifying β-diversity

A feature common across all designs was that variance in β-diversity estimates increased with spatial scale. This could be a result of a decrease of pair-wise point comparisons at large distances and thus a greater influence of outliers, or due to the randomisation of the environmental gradient with respect to the orientation of the sampling designs between runs. If the former is true then studies should remain vigilant of results at the largest spatial scales, and consider, if possible, sampling at scales slightly larger than required to ensure accurate estimates at the scales relevant to ecological analyses and data interpretation. If the latter is true, it becomes more difficult to design field studies, with the recommendation being that studies should attempt to ascertain the direction(s) of any environmental gradient(s) before commencing surveys. However, a multi-directional design, such as those based on fractal patterns, will be more likely to provide accurate β-diversity estimates than a unidirectional sampling design such as transects in situations where we do not know *a priori* the direction of the gradient(s) that are driving species turnover.

Our results from dissimilarity modelling appeared relatively robust to sampling effort, with the spatial orientation of sampling points being a more critical determinant of the observed patterns of β-diversity than sample size. The partitioning of diversity, however, was greatly affected by both configuration and sampling effort. Contributions of α- and total β-diversity (i.e. the sum of all β components) were similar across designs, except in cases of severe undersampling. This can be easily explained as the sampling grain, here one cell, determined the values of α-diversity regardless of sampling effort, which only provided a more accurate estimate of the mean α-diversity, whereas sampling effort

determined the values for γ-diversity (Crist and Veech, 2006). Thus, undersampling will lead to a greater relative contribution of α- than β- to γ-diversity.

In our simulation > 40 points appeared sufficient to adequately estimate γ-diversity. However, where β-diversity was further partitioned into multiple spatial scales, the sampling effort and spatial orientation of sampling points became important. All sampling designs overestimated the contribution of β-diversity at larger spatial scales. In all likelihood, with every additional partition of β-diversity at a larger spatial scale we would need to increase the sampling effort in order to provide an accurate estimate. If this is the case, then we must be careful of confounding the relative importance of large-scale β-diversity in determining community richness and composition patterns with a reduced number of replicates at those scales. Furthermore, in comparisons between studies we should account for differences in sampling grain (the size of the basic unit sampled), sampling effort and sampling point configuration.

2.6.3 Recommendations for sampling community turnover

The accuracy of any estimate of a scale dependent ecological process will depend upon the total area covered and the sampling effort committed (Kallimanis et al., 2002). However, the differences found between sampling designs highlight that the spatial pattern by which data are collected may also affect our estimates of β-diversity. Sampling designs that naturally partition across multiple spatial scales are able to generate a greater resolution and accuracy of diversity patterns than more systematic designs (Fortin et al., 1989). Ideally, we would tailor our sampling designs according to the taxa and the processes we wish to study, but in reality this will rarely be possible because of insufficient pre-existing information about the scales at which those taxa and processes operate. Given that many ecological processes exhibit fractal or multi-fractal patterns (Brown et al., 2002), a sampling design based upon fractals would seem to be an appropriate approximation to the ideal sampling design. We found that a sampling design of triangle fractals was more successful at estimating our two measures of β-diversity than classical ecological sampling

designs, covering a wider range of spatial scales and at higher accuracy. Furthermore, we have shown that the sampling design could be subsampled, reducing sampling effort with little reduction in accuracy while maximising the range of spatial scales that can be covered. Therefore we recommend that future field studies investigating β-diversity utilise a fractal-based sampling design to increase the accuracy of results.

Chapter 3

Optimising bait for pitfall trapping of Amazonian dung beetles

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3.1 Abstract

The accurate sampling of communities is vital to any investigation of ecological processes and biodiversity. Dung beetles have emerged as a widely used focal taxon in environmental studies and can be sampled quickly and inexpensively using baited pitfalls. Although there is now a wealth of available data on dung beetle communities from around the world, there is a lack of standardisation between sampling protocols for accurately sampling dung beetle communities. In particular, bait choice is often led by the idiosyncrasies of the researcher, which leads to difficulties for inter-study comparisons. In general, human dung is the preferred choice, however, it is often in short supply which can severely limit sampling effort. . By contrast, a pig may provide up to twenty times the dung volume. We tested the ability of human and pig dung to sample a primary forest dung beetle community, as well as three mixes of the two baits of different proportions. Analyses focussed on the comparability of sampling with pig or human-pig dung mixes with studies that have sampled using human dung. There were no significant differences between the richness and abundance sampled by each bait. The communities sampled were remarkably consistent across baits, and ordination analyses showed that the communities sampled by mixed dung were not significantly different from that captured by pure human dung, with the communities sampled by 10% and 90% pig mixes structurally most similar to communities sampled by human dung. We suggest that a 10:90 human:pig ratio, or similar, is an ideal compromise between sampling efficiency and the availability of large quantities of bait for sampling Amazonian dung beetles. Assessing the comparability of community samples collected using different baits represents an important step to facilitating large-scale meta-analyses of dung beetle communities collected using non-standard methodology.

3.2 Introduction

Quantifying ecological processes and the effects of anthropogenic disturbance requires us to have an accurate and comparable representation of ecological communities. Inaccurate sampling may lead to spurious conclusions regarding the responses of species to anthropogenic processes and so it is essential that researchers implement appropriate sampling techniques on appropriate indicator taxa.

Dung beetles are emerging as an increasingly popular focal taxon for ecological research (Gardner et al., 2008a, Gardner and Nichols, 2011, McGeoch et al., 2002, Spector and Ayzama, 2003). They are cost-effective to survey (Gardner et al., 2008a), can be rapidly sampled using baited pitfall traps (Spector and Forsyth, 1998), and are sensitive to anthropogenic disturbances and habitat change (Nichols et al., 2007). They also fulfil several important functional roles including secondary seed dispersal, soil perturbation, parasite suppression and nutrient cycling (Andresen, 2002, Nichols et al., 2008), and these functional roles are easy to study and manipulate in the field (Slade et al., 2011, 2007). Furthermore, they may be separated into ecologically meaningful functional groups based upon diel activity and one of three breeding strategies, rollers, tunnellers and dwellers (Doube, 1990, Halffter and Matthews, 1966), that determine rates of dung removal, seed dispersal and germination (Andresen, 2002, Vulinec, 2002).

Dung beetles may be rapidly sampled using inexpensive baited pitfall traps (Larsen and Forsyth, 2005). However, the choice of bait has been largely driven by the idiosyncrasies of individual researchers rather than based upon empirical evidence and this can severely hinder the validity of inter-study comparisons (Spector, 2006). By contrast, a large number of studies have investigated the resource preferences of dung beetle species (Davis et al., 2010, Dormont et al., 2006, Errouissi et al., 2004, Estrada et al., 1993, Gittings and Giller, 1998, Hill, 1996, Horgan, 2008, Howden and Nealis, 1975, Louzada and Carvalho E Silva, 2009, Vernes et al., 2005). Although some species are highly specialised, the majority of dung beetles have wide diet breadths and may be attracted to a variety of

baits, including dung, carrion and rotting fruit and fungi (Larsen et al., 2006). Dung-feeding species in particular seem remarkably generalised and can be trapped with many dung types (Larsen et al., 2006), although the type and size of dung used can have a significant effect on the number of species and individuals captured (Davis et al., 2010, Errouissi et al., 2004, Horgan and Fuentes, 2005, Howden and Nealis, 1975, Martín-Piera and Lobo, 1996, Peck and Howden, 1984, Shahabuddin et al., 2010).

There has been little effort to quantify the abilities of different baits to successfully sample a community and the question remains as to what is the optimal bait choice for ecological research. In general, omnivore dung captures a wider breadth of species than herbivore dung and carrion. Human dung, in particular, seems to sample a greater number of species and biomass than other baits (e.g. Howden and Nealis, 1975, Larsen et al., 2006, Martín-Piera and Lobo, 1996). For example, Larsen et al. (2006) found that all species except one attracted to non-human dung were also sampled by human dung, while collecting five times more individuals and twice the number of species than cow dung. Furthermore, human dung is available across the world wherever the researcher travels. Consequently, it has become the bait of choice in the majority of studies investigating the effects of habitat disturbance, particularly in the neotropics, although cattle and pig dung is also used in Africa and Asia (Boonrotpong et al., 2004, Davis and Philips, 2005). However, a researcher can only provide fresh dung for around eight to ten traps per day, based on a standard bait size of 20 g (pers. obs.). Unless they have particularly obliging companions this can provide a major limiting factor on potential sampling effort.

A domesticated pig, conversely, is likely to produce over 20 times the weight of manure (Brumm et al., 1980), and although not all will be usable as bait, it may nonetheless vastly increase the number of traps a researcher can set. As another omnivore, pig dung may also attract a wide range of species, although to our knowledge the richness of dung beetle communities sampled using pig dung has not been compared against human dung. Furthermore, wild suiformes (pigs and peccaries) are found across the globe and so are a natural source of dung for many species.

If dung beetles do have preferences for specific types of dung, then a mix of two or more dung types may catch a fuller complement of the community and therefore provide a more complete inventory of the dung beetles present than a single dung type. Bait mixes (as opposed to trap arrays that consist of separate pitfalls with different baits) are rarely used (e.g. Estrada et al., 1998) and it remains untested if they capture a wider breadth of species. Here, we examine the efficacy of pig dung and pig-human dung mixes at sampling dung beetle communities compared to sampling with human dung. Given that human baited pitfalls have been implemented in many previous studies, we specifically compare the communities sampled by human dung with those sampled by the mixes and pig dung. A successful bait will sample both a high number of species and individuals, but also a community that is comparable to that collected by human dung to allow for valid comparisons with the previous literature.

3.3 Methods

The study was situated in a large *Eucalyptus* pulp plantation in the Jari region in the north-east Amazon, Pará, Brazil. The Jari plantation consists of ∼65,000 ha of *Eucalyptus* plantations, ∼45,000 ha of regenerating secondary forest and ∼1.5 Mha of largely undisturbed primary forest. The study site was an area of largely undisturbed primary forest, large enough that sites could be considered independent of neighbouring *Eucalyptus* plantations (mean distance of sampling points from *Eucalyptus* = 763 m, range = 443–1057 m).

3.3.1 Dung beetle sampling

We established 25 irregularly spaced sampling points that were separated by ∼100 m to achieve trap independence (mean distance to nearest neighbour = 96.8 m; range = 83.8–122.2 m, Larsen and Forsyth 2005). A baited pitfall trap was placed at each sampling point. Sampling pitfalls (20 cm width, 15 cm depth) were buried flush with the ground and part-filled with a killing solution comprising of water, salt and detergent.

We investigated five bait combinations: a) pure human dung, b) a 10:90 pig-human mix, c) 50:50 pig-human mix, d) 90:10 pig-human mix, and e) pure pig dung. Hereafter we refer to bait mixes only by the percentage of pig dung (10%, 50% and 90%). The bait mixes were homogenised, separated into 20 g gauze parcels and frozen until use. The number of species and individuals may be positively correlated with bait quantity (Peck and Howden, 1984), but 20 g was chosen as this quantity is commonly used in dung beetle sampling (e.g. Gardner et al., 2008b). For each trap, bait was suspended beneath a lid directly above the pitfall. The lid acted as a rain cover as well as limiting the ability of beetles to directly access the bait. Bait type was assigned randomly to each point so that there were five replicates of each bait type.

Sampling was carried out over eight days in the late wet season between 14–22 July 2010. Traps 1–10 were set on the first day and the remaining traps set on the second day, and all traps operated over seven trap nights. Trap contents were collected after two, five and seven days, and bait replaced after two and five days. All individuals collected were oven dried and then identified to species level using a reference collection held at the Universidade Federal de Lavras (UFLA), where all samples were deposited. Species were identified using classifications developed by Vaz-de-Mello and Gardner (2009, unpublished).

3.3.2 Analyses

The attractiveness of traps may be confounded by their location and the order in which they were sampled. If beetles are attracted to dung over distances greater than 50 m, then traps at the edge of the sampling array may capture more individuals than interior traps as they will have fewer near neighbours and therefore sample from a wider neighbourhood. Second, traps that were set on the first sampling day may capture more individuals than traps set on the second due to a potential depletion effect. We investigated if there were significant differences through Welch's t-tests.

Further analyses focussed on the ability of pig dung and human-pig dung mixes to sample the dung beetle community and the similarity of these communities to those sampled by human dung. As pig dung may be available in greater quantities than human dung this may remove limitations in sampling effort whilst maintaining comparability with previous investigations.

We investigated two aspects of a baits ability to efficiently and accurately sample the community. First, we investigated the proportion of the community sampled by each bait. A successful sampling strategy should rapidly capture an almost complete representation of the community. We calculated the mean and total number of species and number of individuals sampled by each bait. We also visually compared trap-based accumulation curves to examine the rate at which species were sampled. Finally, as studies frequently remove species of low abundance prior to analyses, and that these species may also have large influences on richness estimates, we investigated the influence of rare and occasional species on estimates of species richness (Barlow et al., 2010). We determined the number of species in each bait type while sequentially removing singletons, doubletons and so on in order to ascertain their influence on diversity estimates.

Second, we compared the composition of the communities sampled by the pig-based baits with pure human dung bait. As a large proportion of existing surveys have used human dung baits, it is important that any dung mixes sample an equivalent subset of the community to allow for inter-study comparisons. First, we investigated the structure of rank abundance curves for each bait type, maintaining the rank order of species as observed in the traps baited with human dung. If a bait samples a very different community from the community sampled by human dung then the abundance plot will become deconstructed, with changes in the identity of the most abundant species. We also investigated the number of shared species between the pig-based bait communities and the human bait community using Jaccard dissimilarity. Furthermore, we grouped genera into functional groups representing different breeding strategies and patterns of diel activity using pre-existing literature (Feer and Pincebourde, 2005), and investigated if there were clear

differences in the range and structure of functional groups collected by each dung type. We assigned the diel activity for a species within a given genera as the diel activity of the majority of species within that genera. There may be small intra-genera differences in diel activity that are obscured by assigning this functional trait at the level of genus rather than species, however, we lacked species-specific data for all species present at the study site.

Finally, we compared the communities sampled by each bait type using partial canonical ordination (RDA, Legendre and Legendre 1998). We investigated differences in community composition using presence-absence data, and community structure using Hellinger-transformed abundance data (Legendre and Gallagher, 2001). Hellinger transformation accounts for situations where sites that share no species may be geographically closer than sites that do share species (Legendre and Legendre, 1998). *Post hoc* trend surface analysis of community composition found significant spatial autocorrelation in the abundance data (Appendix B.2), and so we controlled for the influence of trap location by holding the spatial coordinates of traps as a constant in the ordinations (Borcard et al., 2011). Significance was tested through permutation tests using 999 randomisations. Analysis of similarities (ANOSIM, Clarke 1993) was used to test for significance differences among

Table 3.1. Diversity indices for communities sampled by two pure dung baits and three mixes (given as the percentage of pig dung). Numbers in parentheses not representing standard errors are absolute values as a proportion of the total number of species recorded by that bait type. Evenness was measured through the Shannon Index.

	Human	10%	50%	90%	Pig
Mean richness (± se)	20.2 (3.02)	26.2 (1.39)	21.8 (2.18)	24.6 (2.54)	20.6 (1.47)
Total species	41	40	35	41	34
% of total species	77.3%	75.5%	66%	77.3%	64.2%
Mean individuals (± se)	114.2 (29.8)	167.8 (20.9)	140.6 (33.4)	159 (26.7)	145.2 (23.3)
Total individuals	571	839	703	795	726
Singletons	12 (29.2%)	6 (15%)	8 (22.9%)	9 (22%)	6 (17.6%)
Doubletons	5 (12.2%)	2 (5%)	3 (8.6%)	3 (7.3%)	5 (14.7%)
Unique species	4 (9.8%)	4 (10%)	1 (2.9%)	3 (7.3%)	1 (2.9%)
Evenness	2.74	2.92	2.63	2.92	2.31

communities. All analyses were performed using program R 2.14.2 (R Development Core Team, 2011) using the 'vegan' package (Oksanen et al., 2012).

3.4 Results

We captured 3,634 individuals of 53 species and 12 genera from 175 trap nights (Table B.1). There was no significant effect on species richness of proximity to the edge ($t = -0.95$, df = 15, $p = 0.36$) or whether traps were in the group of traps set on the first or second day ($t = 1.59$, df = 19.8, $p = 0.13$). Over half of the species (28 of 53) were sampled by all five baits. A further six species were common across four baits. Thirteen species were sampled by one bait only, all of which had ≤2 individuals. Excluding uncommon species with ≤5 individuals (leaving 35 out of 53 species), species sampled were remarkably consistent across all bait types, with baits sampling 94-100% of the common species.

Mean species richness and abundance was greater in the 10% and 90% pig mixes and lower in the two pure baits, as well as the 50% pig mix,however all differences were non-significant (Table 3.1, Fig. 3.1). In total, however, pure human dung sampled a

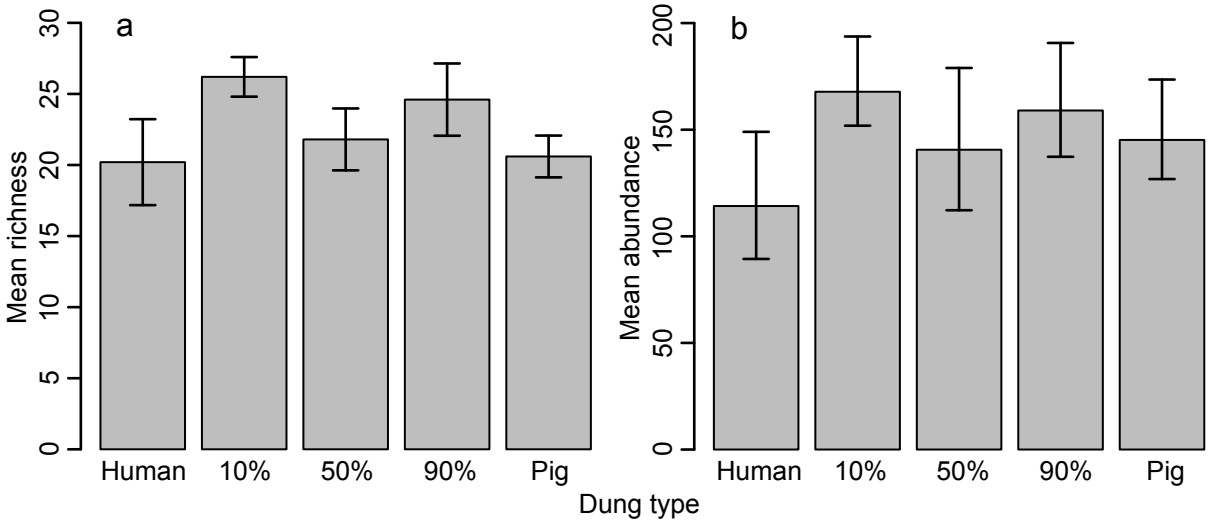


Figure 3.1. Mean species richness (a) and mean number of individuals (b) of dung beetles sampled by each bait type. Pig-human bait mixes are referred to by the percentage contribution of pig dung to the overall mixture. Error bars are standard error

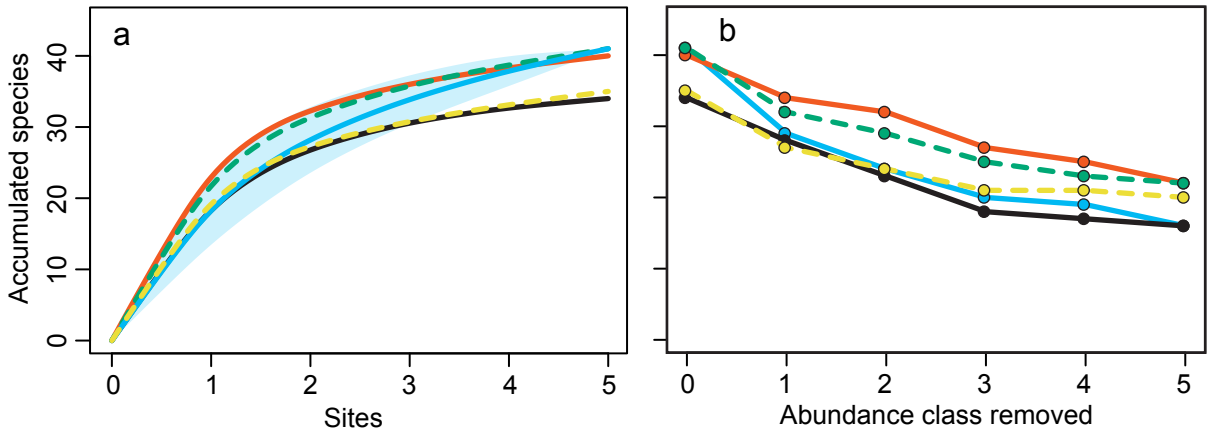


Figure 3.2. (a) Species accumulation curves (lines) for dung beetle communities, and (b) numbers of species sampled by each of five bait types while sequentially removing singletons (abundance class = 1), doubletons (abundance class = 2) etc. The red polygon represents the standard error for human dung. Colours represent dung type: human (blue), 10% pig (red), 50% pig (yellow dashed), 90% pig (green dashed), pig (black).

similar number of species as the 10% and 90% pig mixes (75–77% of the total community sampled; Table 3.1). The site-based accumulation curves showed that the 10% and 90% mixes sampled at a faster rate than other dung mixes, but that pure human dung captured a similar total number of species (Fig. 3.2a). The 50% mix and pure pig dung, however, both accumulated species at a slower rate and had lower total species richness. When rare species were removed, however, pure human dung sampled a relatively low number of species (Fig. 3.2b). Almost 30% of species sampled by human dung were singletons and a further 12% doubletons (Table 3.1). If these species were removed from each bait then the 10% and 90% mixes have a much higher species richness (30 and 33 species respectively) compared to the other baits (23–24 species).

The standardised rank abundance plots showed that common species were sampled by all baits in similar numbers (Fig. 3.3). The identities of uncommon species, however, were variable between baits. The 10% and 90% showed the most similar abundance patterns to human dung. This was reflected in the number of species shared with the human dung community (Fig. 3.4). All baits shared 69-78% of species with human-baited traps, with the 90% pig mix sharing the highest number of species (36).

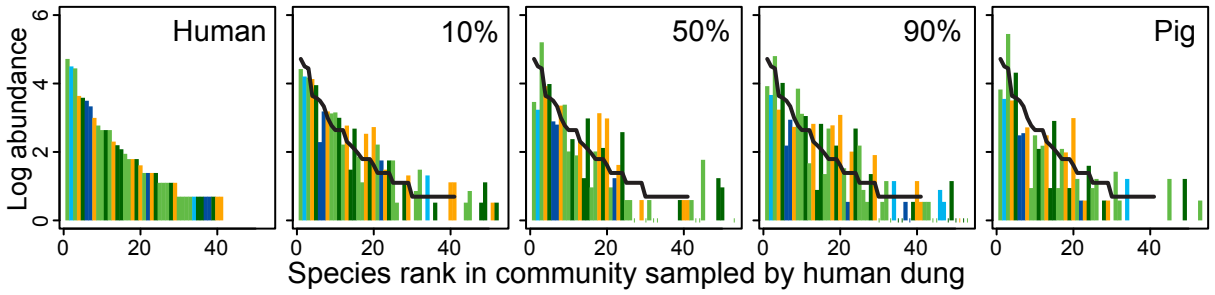


Figure 3.3. Rank abundance plots for species collected by different dung mixes. Bar colours indicate functional group: small rollers (green); large rollers (dark green); small tunnellers (blue); large tunnellers (dark blue); and dwellers (orange). On plots b-e the rank abundance curve for pure human dung has been overlaid (black line) and abundance has been standardised to be equivalent to the total abundance of all species collected by pure human dung. Bars greater than the line indicate species with greater abundances than human dung, and bars below a lower abundance.

All baits trapped a similar richness and abundance of functional groups (Table 3.2), with the exception of large, crepuscular tunnellers, which were present only in pure human dung and the 10% mix. This groups consists of a single genus, *Coprophanaeus*, which are preferentially necrophagous but can occasionally be attracted to carnivorous or omnivorous dung (Edmonds and Zidek, 2010). All three species captured from this genus occurred as singletons. The other inconsistency occurred in the diurnal small roller group that had extremely low abundance in the 50% mix. This was the result of a single species, *Canthon triangularis*, that was very abundant in all other baits but not in the 50% mix, with this results potentially representing a sampling anomaly.

Partial canonical ordination on community composition (presence data) was insignificant (adjusted $R^2 = 0.02$; $p = 0.21$). Ordination on community structure (abundance data) was significant ($p < 0.005$), although the ordination explained just 16% of the variation in community composition. The first axis explained 54.8% of the explained variation and the second axis 28.9%. Analysis of similarities found no significant differences in community composition between dung types, but there were slight differences in community structure between human dung and 50% pig dung (R = 0.376; $p = 0.016$) and pure pig dung (R = 0.364; $p = 0.017$).

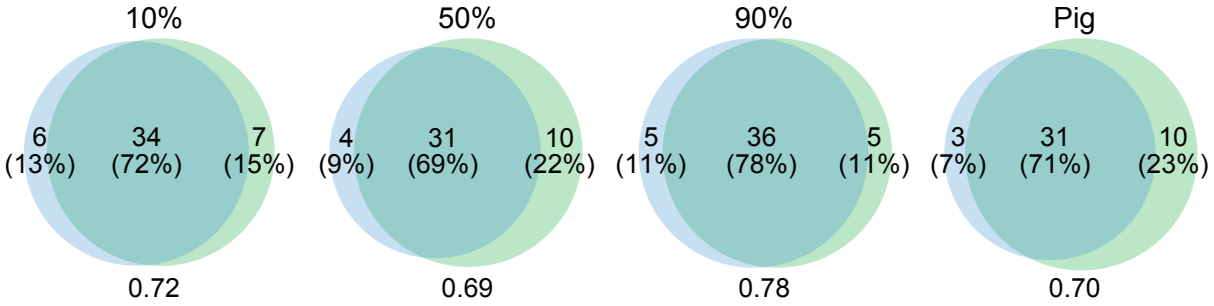


Figure 3.4. Proportional venn diagrams visualising the similarity between the community sampled using pure human dung and the communities sampled by dung mixes. Diagram components represent species unique to pure human dung (green), the number of species unique to the other bait type (blue), and species shared by both (overlap). Numbers below plots indicate similarity values (1-Jaccard) with human dung-baited traps.

3.5 Discussion

Although there were small differences in the number of species and individuals sampled by each bait differences were non-significant. Furthermore, the communities sampled by each bait were remarkably consistent: all pig-based baits shared a very high proportion of species with the human-baited traps (Fig. 3.4); nearly all functional groups occurred in similar numbers in each bait (Table 3.2); and nearly all of the species with 5 individuals were sampled by all baits (Fig. 3.3). Those species that were confined to one or two bait types all occurred at very low abundances. This supports other investigations that have found a high number of generalists in dung beetle communities (Dormont et al., 2006, Larsen et al., 2006). The composition of the communities also did not differ markedly between baits, although there were slight differences in community structure, with the communities sampled by the 10% and 90% mixes statistically consistent with the community sampled by pure human dung. These results confirm that studies sampling using a pig-human dung mix would be comparable to studies using solely human dung bait, with the possibility of greatly increasing sampling effort.

Human dung-baited pitfalls have been shown to outperform herbivorous dung and carrion and fruit for sampling dung beetle communities (Howden and Nealis, 1975, Larsen et al., 2006), however, it has never been tested against pig dung or against dung mixes. Although mean richness was lower, human dung-baited pitfalls did collect an equivalent

Table 3.2. The number of species and individuals captured by each bait type for genera assigned to functional groups based upon breeding strategy and diel activity.

Breeding strategy	Diel activity	Human	10%	50%	90%	Pig
Species richness						
Dweller	Diurnal	9	10	9	9	7
Large roller	Crepuscular	5	3	3	4	3
Large tunneller	Diurnal	3	4	3	3	3
Large tunneller	Crepuscular	2	2			
Large tunneller	Nocturnal	5	5	6	6	5
Small roller	Diurnal	2	2	1	4	2
Small tunneller	Diurnal	10	9	8	10	8
Small tunneller	Nocturnal	5	5	5	5	6
Abundance						
Dweller	Diurnal	81	119	164	129	107
Large roller	Crepuscular	64	54	43	38	30
Large tunneller	Diurnal	21	43	36	58	16
Large tunneller	Crepuscular	2	2			
Large tunneller	Nocturnal	53	88	97	108	122
Small roller	Diurnal	90	101	3	59	46
Small tunneller	Diurnal	33	65	55	108	27
Small tunneller	Nocturnal	227	268	278	250	369

total number of species to the human-pig mixes, and more than traps baited with pure pig dung. This was primarily due to the large number of singletons and doubletons collected by human dung and the relatively slow rate of species accumulation, suggesting that a large number of species are only occasionally attracted to human dung whereas they may be caught in higher numbers by pig mixes (see the bars in Fig. 3 for bait mixes that extend above the standardised rank abundance curve for the human-baited traps). Many studies exclude species with low abundance as although they may represent species that are naturally rare within the environment, they may also represent transient, tourist species (e.g. Davis et al., 2010, Errouissi et al., 2004, Viljanen et al., 2010). However, excluding these uncommon species may have important consequences for the interpretation of ecological results (Barlow et al., 2010). Almost 30% of species sampled by human dung were singletons and a further 12% doubletons (Table 3.1). In fact, if singletons were removed, then human dung-baited pitfalls collected no more species than those baited by pig dung.

3.6 Conclusion

The richness, individual abundance, composition and structure of communities sampled by pig-human dung mixes were comparable to those sampled using pure human dung. From the baits that we tested, the 10% mix sampled the greatest number of species and individuals, and was compositionally closest to that of human dung. However with only a small addition of pig dung (2 g in a 20 g bait) there will still be practical issues with the availability of human dung that limit the number of traps that can be set. We recommend from these results that a 90:10 pig to human ratio, or similar, represents a suitable compromise between appropriately sampling the dung beetle community, comparability with existing studies and the availability of large quantities of dung to facilitate expansive trap networks.

Our study investigated just two bait types at one location in Amazonian primary forest, yet nonetheless represents important information on the ability of dung mixes to adequately sample dung beetle communities. Further effort is required to test different dung types in different habitats and different continents with different pools of suitable bait sources to ascertain whether any particular bait or bait mix can be used in all investigations at any location. Dung beetles are a promising indicator taxa for ecological research (Gardner and Nichols, 2011, Spector and Forsyth, 1998) and there have been recent attempts to carry out meta-analyses on the vast quantities of data already collected (Nichols et al., 2007). Assessing the comparability of community samples collected using different baits, as we have done here, represents an important step towards facilitating rigorous comparisons among studies that have investigated the same taxon but without a standardised sampling protocol.

Chapter 4

Morphological traits interact with habitat to determine the scale and drivers of the spatial structure of Amazonian dung beetle communities

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4.1 Abstract

We investigated the drivers structuring dung beetle communities in primary, secondary and *Eucalyptus* forest in the north-eastern Amazon, Brazil. We took a spatially explicit approach, analysing communities at multiple spatial scales, and linking the scales at which communities were structured with body and wing morphology. First, we identified two distinct functional groups based upon morphological traits that govern flight ability and foraging strategy: a small species group with low wing loading and high manoeuvrability that favours perch-and-wait foraging over small areas, and a large species group with high wing loading and low manoeuvrability that favours continuous flight foraging over large areas. For a subset of species we then determined the spatial scales that were most important in structuring their distributions. The distributions of small species were structured at larger scales than large species. Second, we estimated the relative influence of environmental and spatial drivers on the communities of each trait group at three spatial scales through variation partitioning. Space was more important than environment in structuring dung beetle communities but there was variation between morphological groups and habitats. The small species community had greater variation at fine scales, particularly in secondary forest, whereas the large species community responded to variation at medium- and broad-scales. Environmental drivers explained a large amount of variation in communities in *Eucalyptus* plantations, particularly in the small species community. We found that the drivers governing the spatial distributions of dung beetle species and communities were dependent upon morphological traits governing foraging strategies and dispersal ability. Furthermore, different guilds may respond differently to habitat modification and at different spatial scales.

4.2 Introduction

The spatial turnover of community composition, β-diversity, is critical for the processes maintaining biodiversity (Condit et al., 2002), and provides a direct link between local and regional diversity (Anderson et al., 2011, Gering and Crist, 2002). Both niche and neutral processes may act in tandem to control patterns of β-diversity (Legendre et al., 2005), and the relative importance of these drivers may be scale- (Laliberté et al., 2009) and taxa-dependent (Nielsen et al., 2012).

Variation partitioning allows us to decompose these drivers into separate, additive components, such as the variation explained by environmental variables and the variation explained by spatial structure (Borcard et al., 1992). Through the relative contributions of different components, we can begin to elucidate the relative importance of different drivers of β-diversity, and we may consider that the variation in community composition explained by space may be attributed to neutral process, and the variation explained by environmental or topographic variables can be attributed to niche-partitioning (Dray et al., 2012, Legendre, 2008, Legendre et al., 2005). Furthermore, we may partition this variation at a number of spatial scales to examine scale-dependent processes acting on the community (Ali et al., 2010, Laliberté et al., 2009, Zhang et al., 2010).

Using these techniques, we sought to investigate two aspects governing the spatial structure of a dung beetle community in the north-eastern Amazon: (1) at what scales do the processes that generate spatial patterns of diversity operate and how does the relative contributions of these processes vary with spatial scale?, and (2) whether the relative contributions of different processes is dependent upon the morphological traits of species composing the community. Recognising that different components of the community may respond to different drivers and at different spatial scales, we subset the dung beetle community in order to examine how body and wing morphology that can be linked to flight ability and foraging strategies alter the relative importance and spatial scale of these drivers.

4.2.1 Dung beetles and flight ability traits

Dung beetles are an ideal focal taxon for diversity studies (Gardner et al., 2008a, Spector, 2006). Many dung beetle species have strong habitat associations (Andresen, 2005, Davis et al., 2002, Escobar et al., 2007, Hill, 1996), and may respond strongly to changes in vegetation structure (Davis et al., 2001, Lumaret and Kirk, 1991), soil composition (Davis et al., 2008, Doube, 1991, Sowig, 1995), microclimate (Lobo et al., 2002) and exhibit strong responses to habitat change and fragmentation (Nichols et al., 2007). These responses may also vary between functional groups (Louzada et al., 2010).

We therefore have a good understanding of the environmental predictors driving local patterns of dung beetle diversity. However, we know less about the role played by space and neutral processes, and so we must also investigate the spatial scales at which dung beetles forage and disperse, as well as the scales at which populations are spatially structured. The speed, range and agility with which dung beetles can travel may be particularly important as dung resources are unevenly spaced and ephemeral and therefore there is often extreme competition for resources (Horgan, 2001, Horgan and Fuentes, 2005). Consequently, wing morphology of dung beetles may be correlated with an individuals ability to rapidly access dung.

Although data are lacking for dung beetles, in other taxa wing morphology has been found to be a significant predictor of lifestyle strategies. In general, large wing size, which is positively correlated with body size (Gibb et al., 2006), allows for larger foraging distances (Araújo et al., 2004) and greater dispersal (Berwaerts et al., 2002), and consequently lower β-diversity (Soininen et al., 2007a). High wing-loading (large body size and relatively small wings) infers a higher flight speed with lower manoeuvrability and therefore favours extended flight (Betts and Wootton, 1988). Low wing loading (small body size relative to wing size) infers greater flight ability and manoeuvrability, which may allow individuals to occupy habitats unsuitable for others, such as densely vegetated areas (Kalcounis and Brigham, 1995).

Dung beetles fall into two categories of resource attribution that may be linked to characteristics of body and wing morphology (Gill, 1991, Howden and Nealis, 1978). First, small-bodied species, mostly <10 mm in body length, adopt a perch-and-wait strategy (Howden and Nealis, 1978). They have low wing-loading and slow flight that allows them the high manoeuvrability necessary to land on leaves, waiting until resources become locally available (Gill, 1991). Some arboreal species have even adapted to perching and waiting on the actual source of dung, living phoretically in the fur of monkeys and sloths (Halffter and Matthews, 1966, Herrera et al., 2002, Jacobs et al., 2008). However, the slow flight necessary to allow for this agility confers them little competitive advantage in reaching dung from large distances and so it is likely these species have small foraging distances. The limited studies available on tropical dung beetle dispersal distances have focussed on these small species and found individuals typically remain within a few tens of metres of the point of capture which would confirm this prediction (Arellano et al., 2008, Larsen and Forsyth, 2005, Viljanen, 2009). They are, therefore, likely to have more aggregated distributions (Hanski and Cambefort, 1991, Quinn et al., 1994) and so space may be more important in determining their distributions than environmental drivers.

The second strategy belongs to larger-bodied species with high wing-loading that enables fast flight but low manoeuvrability (Howden and Nealis, 1978). This favours continuous flight (Betts and Wootton, 1988) and so it is likely these species forage over much larger distances, although this remains to be investigated in tropical species. We cannot determine the exact foraging distances of a larger range of species without extensive capture-recapture studies, however, by investigating the spatial scales that are most important in the structuring of species abundance patterns we may be able to determine morphological traits that infer the range of distances over which individuals are functioning.

4.2.2 Characterisation of spatial structures

In order to investigate the spatial scales of the processes structuring dung beetle communities we generated a set of spatial variables using a Moran's eigenvector maps framework

(MEM, Borcard and Legendre 2002). The method is a particular class of MEM, labelled distance-based Moran's eigenvector maps (DBMEM) that uses a truncated matrix of the distances between all sampling points and deconstructs the spatial coordinates into eigenvectors that correspond to variation at different spatial scales through principle coordinates analysis. The DBMEM method was previously classed as principle coordinates of neighbour matrices (PCNM) until it was found that PCNMs were a particular case of MEM, and so hereafter we refer to them as DBMEMs under recommendation from Dray et al. (2006), but with the guidance that they are frequently termed PCNMs in the literature.

Using DBMEMs to describe the spatial structure of our communities has several advantages over geostatistical techniques such as traditional trend surface polynomial regression (Bellier et al., 2007), and as a design-based approach is particularly suited to our fractal-based sampling scheme. First, they are able to model spatial structures at a wider range of spatial scales, whilst maintaining the ability to model fine-scale processes of any spatial structure (Borcard and Legendre, 2002). Second, eigenvectors constructed from DBMEM are ordered by the size of the patterns they describe (Borcard et al., 2004). As they are orthogonal they can be combined into additive scale-specific models (Borcard and Legendre, 2002, Borcard et al., 2004). Therefore we can decompose our global DBMEM model into subsets that correspond to variation at only fine, or only broad scales which can then be used as explanatory variables in regression or ordination analyses. This allows us to adopt a multi-scale approach, using each spatial DBMEM subset to partition the variation in dung beetle communities at that particular scale (Laliberté et al., 2009).

4.3 Methods

4.3.1 Study site

The study was carried out at the Jari forestry project in the north-eastern Amazon, Brazil (00°27′–01°30′S, 51°40′–53°20′W), which provides a very large (1.7 Mha) quasi-experimental landscape of ∼65,000 ha of *Eucalyptus* plantations and 45,000 ha of cleared

land and secondary forest (as of 2011, Appendix C.1), embedded within largely untouched primary forest (see Barlow et al. 2007b for greater detail).

We sampled in three habitats: primary forest, a block of 17–25 year old secondary forest and a 2–3 year old *Eucalyptus* plantation (plantations are cut after a 4–5 year cycle). All points were located >0.95 km from the nearest adjacent habitat to avoid the potentially confounding impacts of edge effects and sites were sufficiently far part as to be independent of spatial autocorrelation effects (mean distance among points in different habitats = 14.9 km; range = 7–23 km; Koenig 1999).

4.3.2 Sampling design

We sampled dung beetle communities using a sampling pattern designed explicitly for investigating β-diversity (Ewers et al., 2011, Marsh and Ewers, 2012). Simulations found that such designs were able to estimate β-diversity more accurately at both fine and broad scales than classical sampling designs (Marsh and Ewers, 2012). The design is based upon a fractal pattern of repeated equilateral triangles that simultaneously sample across four spatial scales while maintaining estimates of β-diversity at the smallest scale at all locations (Fig. 4.1).

To generate a full sampling design, a sampling point is located on each apex of a 1st order triangle (Fig. 4.1a). Equilateral triangles are used as three points are the minimum required to generate an estimate of mean β-diversity, and the variance around that estimate. Three 1^{st} order triangles are then located around the apices of a larger 2^{nd} order triangle, giving nine sampling points around the 2^{nd}-order triangle. Three 2^{nd} order triangles, each with three 1^{st} order triangles and nine sampling points, are then arranged on the apices of a 3^{rd} order triangle and so on. For this study we covered four spatial scales, with triangles of side lengths of $10^{1.5}, 10^{2}, 10^{2.5}$ and 10^{3} m for the 1^{st} order through to 4^{th} order triangles respectively.

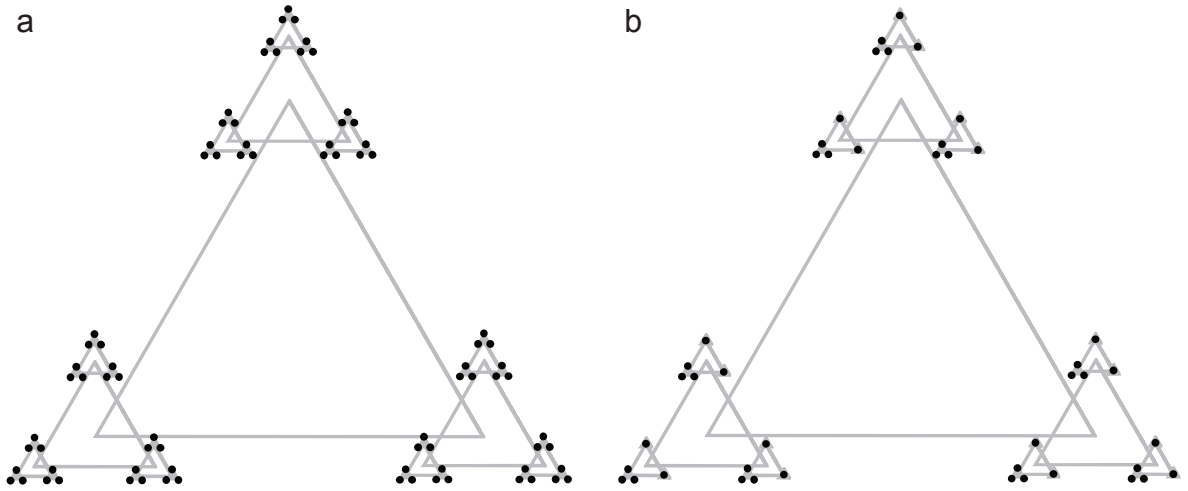


Figure 4.1. The fractal sampling designs employed in the study. Black points represent sampling locations. (a) A full sampling design with a sampling point located at each apex of every 1st order triangle, replicated at four spatial scales. (b) The compromise subsampling design used in the study that reduces the sampling effort whilst maintaining the ability to estimate β-diversity at all spatial scales.

For each of the three control sites, we adapted the full sampling design to reduce sampling effort with little loss in statistical rigour. By replacing two of the 1st order triangles on the apices of the 2nd order triangle with a single point, our subsampling design (Fig. 4.1b) allowed us to reduce the number of sampling points by almost a half whilst maintaining the ability to estimate β-diversity at all spatial scales. In simulations this was found to be the optimal compromise between sampling effort and accuracy of β-diversity estimates (Marsh and Ewers, 2012).

4.3.3 Dung beetle sampling

We sampled dung beetles twice at each site, once in the early dry season (Jul–Oct 2010), and then repeated in the early wet season (Feb–Apr 2011). A baited pitfall trap (20 cm width, 15 cm depth) was placed at each sampling point and buried so the top was flush with the ground. Traps contained a killing solution of water, salt and detergent and were baited with 20 g of pig and human dung in a 90:10 ratio that was found to be the most effective bait in the study area (chapter 3). Traps were operated for 4 days, re-baiting after 2 days which has previously been found to adequately describe the community in this

location (Gardner et al., 2008b). Contents were collected after 2 and 4 days, and all data for each trap was pooled for analyses. Specimens were oven dried before identification to species level using a reference collection at Universidade Federal de Lavras (UFLA). Unknown species were classified according to morphospecies identified by Vaz-de-Mello and Gardner (2009, unpublished).

4.3.4 Morphometric measurements

We selected five individuals from 37 species and 11 genera for morphometric analyses, representing 60-90% of the species and number of individuals in all habitats (62%, 69% and 60% of species; and 82%, 95% and 63% of individuals in primary, secondary and *Eucalyptus* forest respectively). Specimens were taken from the Jari collection housed at UFLA. Specimens were first weighed to 0.0001 g, and body length and width measured with digital callipers. To extract wings specimens were softened in 150 ml of water with 10 g of potassium hydroxide and heated to 100°C for 20 minutes (body length >8 mm) or 10 minutes (body length <8 mm). Wings were removed at the base and further softened with potassium hydroxide for two minutes before stretching on to white paper, and then dried at room temperature for 10 days. All wings were digitised along with a ruler for calibration. Measurements of wing length and width were calculated in SideLook 1.1 (Nobis, 2005). We calculated wing area and wing perimeter using the ImageJ software Fiji (Schindelin et al., 2012).

We used these measurements in order to generate a further four indicators of foraging range: a) wing aspect ratio (wing span^2 ÷ wing area); b) wing loading (body weight ÷ wing area); c) an estimate of flight speed (46.9 × aspect ratio$^{-2.27}$; Dudley and Srygley 1994); and d) an estimate of manoeuvrability (((wing length aspect ratio) ÷ wing length) ÷ 1000). We removed one outlying species, *Coprophanaeus lancifer*, from subsequent analyses as it was almost three times the size of the second largest species. It is a necrophageous beetle, and only a single individual was captured by the baited pitfalls.

4.3.5 Environmental variables

We collected five environmental variables that characterised each site: understory vegetation density; canopy cover; mean and maximum canopy height, and soil composition. We estimated understory vegetation density by taking a digital photograph of a 1 × 1.5m black sheet from a distance of 5 m, held perpendicular to the ground and with the bottom flush with the ground. The sheet was placed ≤5 m from the trap where vegetation remained undisturbed and two photos were taken, one from each direction. The percentage vegetation cover was determined for each photo using SideLook 1.1 (Nobis, 2005) and the mean taken of the two photos.

We estimated canopy cover from digital hemispheric photos taken one metre above the ground directly above each trap (Englund et al., 2000). Percentage cover was determined using Gap Light Analyzer 2.0 (Frazer et al., 1999) using the inner 30 degree ring. We estimated mean and maximum canopy height within a 10 m radius of each trap. We carried out granulometric analyses on soil samples from each site to determine the percentage sand, which has been found to be the most important soil characteristic in determining dung beetle distributions (Davis et al., 2008, Doube, 1983). Soil samples were taken from the spill excavated to bury the pitfall traps, selecting soil that was located immediately below the ground surface.

4.3.6 Statistical analyses

Statistical analyses fell in to four parts (Fig. 4.2): (1) We assigned species to trait-based groups based upon wing and body morphology. (2) We validated that these trait-based groups produced subsets that were spatially meaningful by estimating the spatial scales that species' distributions were structured. (3) For each habitat we decomposed the spatial distribution of sampling points into DBMEMs representing subsets of spatial scales. (4) Finally, we partitioned the variation for the distribution of each morphometric group at each spatial scale subset in to environmental and spatial components.

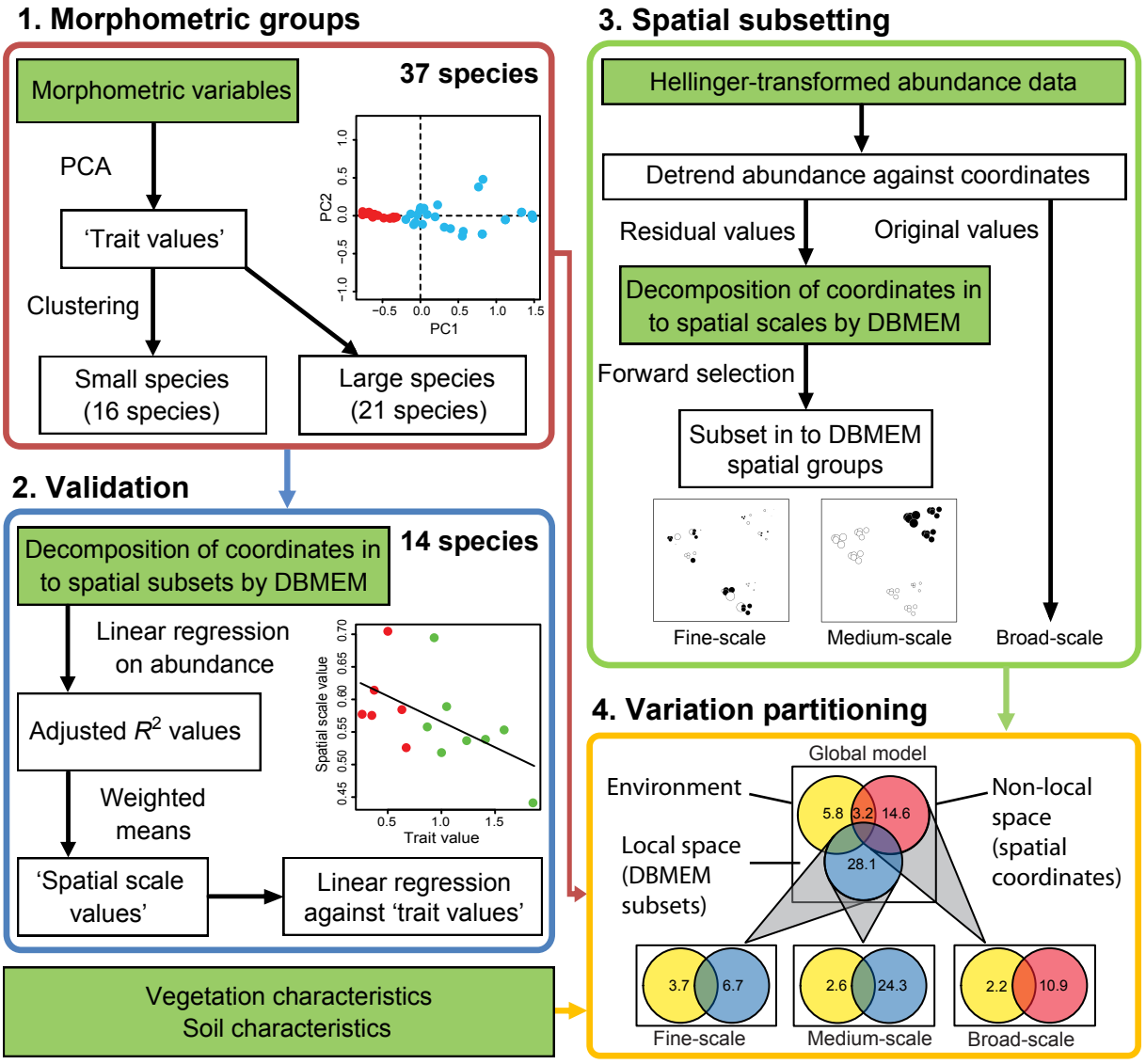


Figure 4.2. Flow diagram of statistical analyses. Green boxes indicate the input of raw data. We used a subset of 37 species for analyses. 'Validation' was carried out with only the primary forest data.

4.3.6.1 Characterisation of trait-based groups

All morphometric variables were found to be significantly correlated (all Pearson's r values >0.92; Appendix C.2). Therefore we characterised the morphology of each species through a principle coordinate analysis (PCA) using all eight raw morphological variables (i.e. not including the four derived metrics of foraging range). For each species we took the values from the first principle components axis as a 'trait value'. We then applied weighted arithmetic average clustering on a Euclidean distance matrix of the species scores

from the PCA. We used the resulting dendrogram to group species into morphometric subsets.

4.3.6.2 Species-level spatial structuring

We do not know at what spatial scales dung beetles range and therefore whether or not the morphometric subsets are likely to correspond to the spatial structure of their distributions. Therefore, we first sought to validate the species groupings by estimating the spatial scales at which ecological processes were determining the patterns of individual species distributions. If these scales correlate with morphometric characteristics, we can subset our communities into species with morphological traits that respond to fine scale variation and those with morphological traits that respond to broad scale variation. We carried out the validation using only the primary forest data. We selected 14 species for which we captured $\geq$10 individuals in $\geq$5 traps and for which we had morphometric data. This represented 28% of species but 76% of individuals captured at this site.

To determine the spatial scales at which species' populations were structured we took advantage of the hierarchical nature of DBMEMs; subsets of DBMEMs remain independent and can be analysed separately, but their explained variation is additive (Ali et al., 2010). To generate the DBMEMs we first created a Euclidean distance matrix of all pairwise distances between sampling points. This matrix is truncated to a threshold distance, set as the minimum distance that keeps all sampling points connected (Borcard and Legendre, 2002). In our triangle fractal design this is equivalent to the distances between the 3^{rd} and 4^{th} order triangles ($\sim$580 m) and thus eigenvectors would not be able to detect information at finer scales (Borcard et al., 2004). In order to detect features smaller than the widest gap in the DBMEM analyses we added six dummy sampling points to fill in the larger gaps (Fig. 4.3a) and allow us to reduce the truncation distance to the distances between the 2^{nd} and 3^{rd} order triangles ($\sim$200m) and thus construct finer scale eigenvectors (Borcard and Legendre, 2002, Borcard et al., 2004). The six dummy sampling points were then removed after the creation of the DBMEMs for subsequent analyses. There

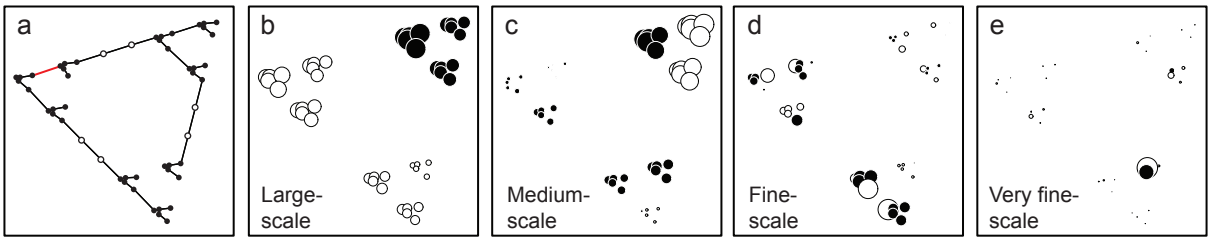


Figure 4.3. Examples of the decomposition of spatial coordinates into different spatial scales using distance-based eigenvector mapping (DBMEM). (a) A threshold distance was taken as the maximum distance (red line) that connected all sampling points (closed circles) in the spanning tree. Dummy sampling points (open circles) were used to 'fill the gaps' in the sampling scheme, and so allow a smaller threshold distance. The distances were decomposed into DBMEMs representing decreasing spatial structures. Each DBMEM can be represented as an eigenvector map (b–e). Bubble sizes ('area') represent the absolute values of eigenvectors; black bubbles are positive values and white bubbles negative values. The spatial scale of each DBMEM was quantified by calculating the total 'area' of the bubbles. DBMEMs were partitioned in to four spatial groups depending on the total area: large-scale (lower DBMEMs), medium-scale (middle DBMEMs) and fine-scale (upper DBMEMs) and very-fine scale (final DBMEMs). In addition, we modelled a fifth scale, broad-scale, representing linear trends of logged abundance against raw spatial coordinates (not shown).

is, however, a resulting tradeoff in some lack of orthoganality between eigenvectors, although this is expected to be small (Borcard et al., 2004). Once the threshold distance was determined, Borcard and Legendre (2002) demonstrated that it is optimal to set all distances in the matrix greater than this distance to four times the threshold distance. Finally, a principle coordinate analysis was carried out on the truncated distance matrix to compute the DBMEM set.

We modelled patterns of species abundances against five spatial scales. The largest scale was variation attributed to scales larger than the sampling extent, calculated as a linear regression of log-transformed abundance against the spatial coordinates of the sampling points. The remaining four scales were generated by decomposing the global DBMEM model into subsets. Subsetting DBMEMs is an arbitrary process that will vary between studies and taxa. We used two measures to separate the DBMEMs into natural groups: the spatial scale that the DBMEM describes, and the Moran's I value. As our sampling points are irregularly spaced, we adopted the approach by Ali et al. (2010). Each DBMEM has a specific value for each sampling point that can depict positive or negative

autocorrelation (the bubbles in Fig. 4.4). The spatial scale that a DBMEM represents can be thought of as the combined 'area' of these bubble values, such that DBMEMs with large total areas were describing broad-scale processes (e.g. Fig. 4.3b) and DBMEMs with small total areas were describing fine-scale processes (e.g. Fig. 4.3e) and so can be separated into similar spatial subsets. Once the DBMEMs were ascribed to the five spatial subsets we quantified the spatial scale of each subset as the mean of the total areas of each DBMEM within that subset. We do not know the spatial scale of the largest scale (the linear trend) except that it is larger than the spatial extent of our study (DBMEM 1; 0.795 ha), and so it was arbitrarily set at a higher value (1 ha).

For each species we regressed log-transformed abundance against the DBMEMs in each spatial subset (Laliberté et al., 2009). We can determine the contribution of each spatial subset to the variation in abundance by the adjusted coefficient of determination (R^2_α) and therefore estimate which spatial scale(s) are most important to the structuring of that species (Ali et al., 2010). A high R^2_α for a spatial subset would mean that the distribution of the species was strongly structured at that spatial scale. Although using R^2_α loses the among-model additive properties of the R^2 (the R^2 of each subset should sum to the R^2 of the global model (Ali et al., 2010)), it allowed us to quantitatively compare subsets among models with different numbers of DBMEMs. For a given species the five regressions generated five R^2_α values, each for a spatial subset, which we plotted against patch area. We condensed these plots into a single 'spatial scale value' by calculating the mean patch area weighted according to the R^2_α values (see Appendix C.5). The 'spatial scale value' therefore represents the dominant spatial scale at which a species is structured. Finally, we ascertained if the wing and body morphology of dung beetles determines the spatial scales at which species are structured by regressing spatial scale values against trait values.

4.3.6.3 Creation of spatial subsets for variation partitioning

In order to ascertain the drivers of dung beetle community composition we used variation partitioning (Borcard et al., 1992), which allowed us to decompose the explained variation in the spatial patterns of community composition into that explained by environment and that explained by space. We first Hellinger-transformed all abundance data, which accounts for situations where sites that share no species can be geographically closer than sites that share species (Legendre and Legendre, 1998) and are particularly suited for canonical partitioning of species abundance data (Legendre and Gallagher, 2001). We also checked the abundance data for linear trends with the spatial coordinates of the sampling points, which indicate the presence of broad, non-local spatial structures that exceed the scale of the sampling extent (Borcard et al., 2004). These spatial structures would compromise the detection of finer-scale structures as half the DBMEMs would be used to model structures broader than the sampling extent (Borcard et al., 2004). We carried out a linear regression of Hellinger-transformed abundance against the spatial coordinates and retained the residuals as detrended abundance. We also retained non-detrended abundance for partitioning at non-local scales.

We created DBMEMs using the same methods outlined earlier, including for secondary and *Eucalyptus* forest. However, in variation partitioning, a large number of spatial predictors may inflate the variation explained by spatial patterns at the expense of that explained by environmental features (Gilbert and Bennett, 2010, Peres-Neto and Legendre, 2010), and so it is important to reduce the number of DBMEMs to those that explain a significant amount of variation. We applied forward selection with a double stopping criterion (Blanchet et al., 2008) on all DBMEMs using the detrended abundance data and retained those that were significant, including negative DBMEMs. Negative DBMEMs are often excluded from analyses, however they are usually related to specific biotic processes, such as competition and dispersal (Dray et al., 2006), and so were included here (Ali et al., 2010).

The spatial subsets of DBMEMs were created as before except in reduced number due to the limited quantity of DBMEMs after forward selection. We created two DBMEM subsets of local space to join the non-detrended non-local space: a) medium-scales (area >0.45 ha; MC >0.9) that represented positive eigenvectors; and b) fine-scales (area <0.2 ha; MC <0) that represented negative eigenvectors.

4.3.6.4 Variation partitioning of spatial turnover in beetle communities

For each morphological group we carried out four partitioning analyses with the Hellinger-transformed abundance data as the response variable. First, we separated species in to the two morphological trait groups. For a given group, we created a global model, using the non-detrended abundance data, and partitioned the variation into three components: that explained by the environmental variables (vegetation and soil); that explained by all the DBMEMs (local space); and that explained by the spatial coordinates (non-local space).

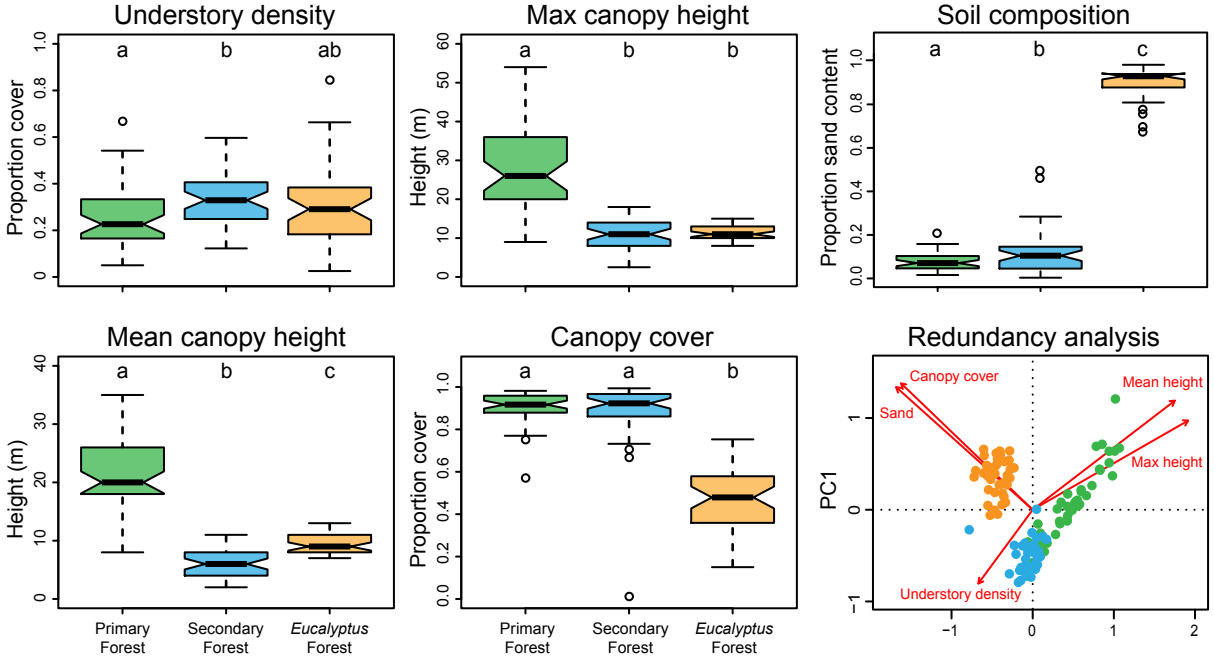


Figure 4.4. Vegetation characteristics of the three habitats: primary forest (green), secondary forest (blue) and *Eucalyptus* forest (orange). Boxes are the first to third quartiles and horizontal lines are median values. Whiskers extend up to 1.5 times the interquartile range and points outside 1.5 times the interquartile range (open circles) indicate outliers.

We further partitioned the global models into the three spatial scales whilst retaining the environmental variables. The non-detrended abundance data was partitioned along with the spatial coordinates and represents non-local 'broad-scale' variation that occurred at larger extents than our sampling design can quantify. The detrended abundance data was decomposed into two local scales, 'medium-scale' and 'fine-scale', by using the two separate DBMEM spatial subsets. Significance of each fraction was tested following Peres-Neto et al. (2006) by calculating the R^2_α from canonical redundancy (RDA). The significance of the pure fractions was calculated through subtraction. We then repeated these analyses for each morphological group in each of the three habitats.

All analyses were performed using program R 2.14.2 (R Development Core Team, 2011). Hellinger transformations, ordinations and variation partitioning were carried out with the 'vegan' package (Oksanen et al., 2012), DBMEM eigenvectors were created with the 'PCNM' package (Legendre et al., 2012) and forward selections were carried out in the 'packfor' package (Dray, 2011).

4.4 Results

We collected 5,604 individuals (primary = 1,468; secondary = 2,284; *Eucalyptus* = 1,852) from 70 species (primary = 50; secondary = 35, *Eucalyptus* = 25) over 1,000 trap nights (Appendix C.3). Vegetation characteristics varied between habitats (Fig. 4.4). Secondary forest had a similar canopy height to *Eucalyptus* forest but canopy cover was much higher and similar to levels in primary forest. Understory density was similar across habitats. Soil sand content was similar between primary and secondary forest, but soil had a much higher sand content at the *Eucalyptus* site.

4.4.1 Morphometric analyses

The first principle axis of the PCA on the morphometric variables explained 93.7% of explained variation (Fig. 4.5b). All measured morphometric variables were highly correlated with first axis trait values (R^2 = 0.94–0.99, Appendix C.4). There were also

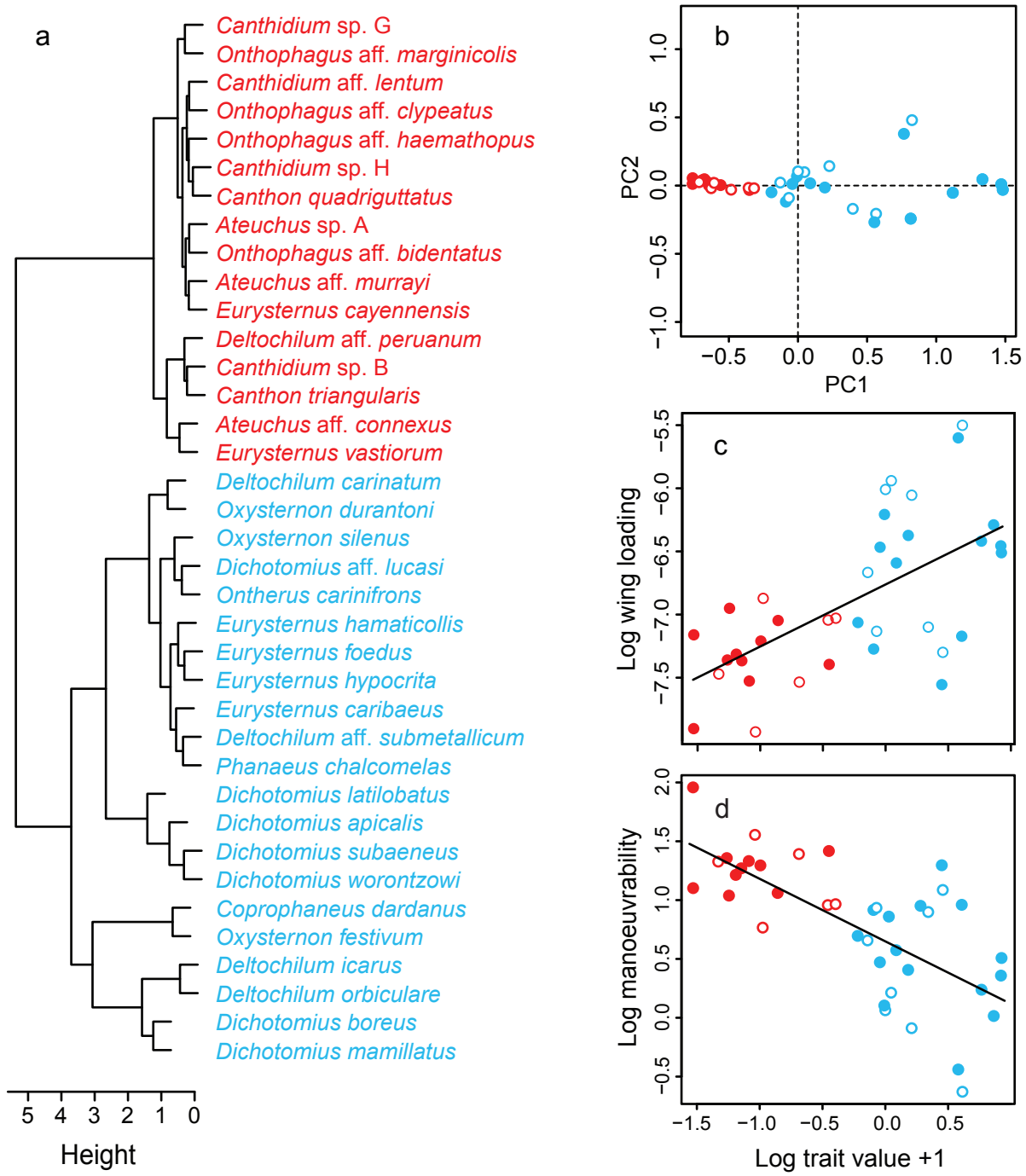


Figure 4.5. We measured morphometric traits for 37 dung beetle species. (a) Clustering analysis revealed two groups: small species <0.05 g (red) and large species >0.05 g (green). (b) We defined 'trait values' as the first axis values after principle coordinates analysis on the morphometric variables. Trait values were significantly correlated with wing loading (c) and manoeuvrability (d). Open circles are species for which we determined weighted mean 'spatial scale values'.

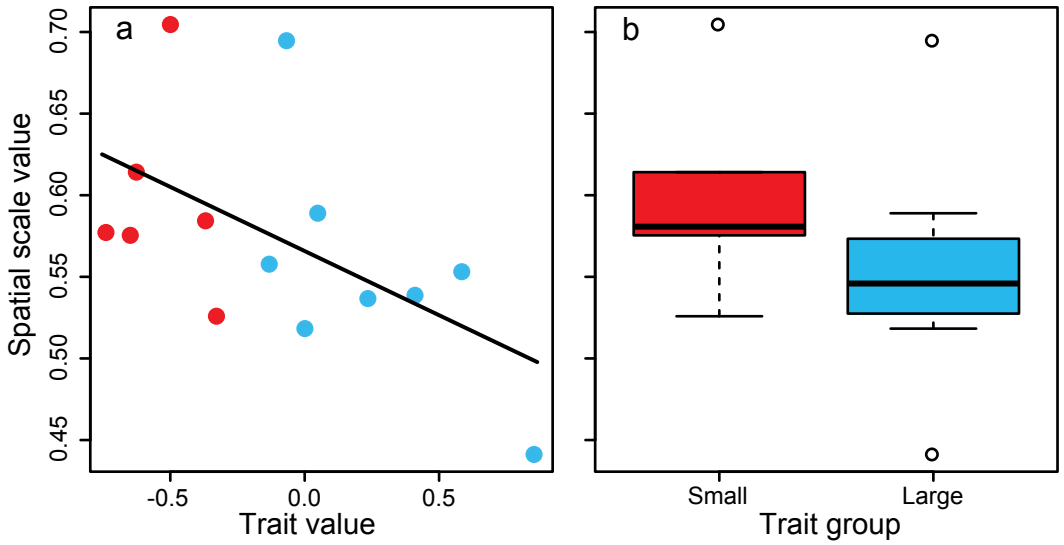


Figure 4.6. Spatial scale values (weighted R^2_α means) plotted against trait values (first principle component axis values) for the small species group (red) and large species group (green) as (a) a regression and (b) a boxplot. Boxes are the first to third quartiles and horizontal lines are median values Whiskers extend up to 1.5 times the interquartile range and points outside 1.5 times the interquartile range indicate outliers (open circles).

significant correlations with the derived foraging range metrics for wing loading (slope = 0.51; $F_{1,35} = 22.66$; p <0.005; Fig. 4.5c) and manoeuvrability (slope = −0.55; $F_{1,35} = 34.02$; p <0.005; Fig. 4.5d) but not for aspect ratio (slope = −0.035; $F_{1,35} = 1.32$; $p = 0.26$) or speed estimates (slope = 0.081; $F_{1,35} = 1.32$; $p = 0.26$). Clustering analysis on the trait values generated two groups (Fig. 4.4): small species (<0.05 g, <0.11 mm), with low wing-loading and high manoeuvrability; and large species (>0.05 g, >0.11 mm) with high wing-loading and low manoeuvrability. These sizes closely coincide with the thresholds given by Howden and Nealis (1978) for species that adopt perch-and-wait strategies and those that actively forage. Genera were largely confined to a single group, except for *Eurysternus* and *Deltochilum* that had species in both groups (Fig. 4.5a).

Spatial scale values (the weighted R^2_α means) were significantly correlated with trait values (Fig. 4.6a). The slope was negative (slope = −0.078, $F_{1,12} = 5.39$, $p = 0.039$) indicating that the distributions of small species responded to larger scale processes than large species. There was, however, no significant difference between the spatial scale values of the small species group (mean = 0.60) and the large species group (mean = 0.55; t =

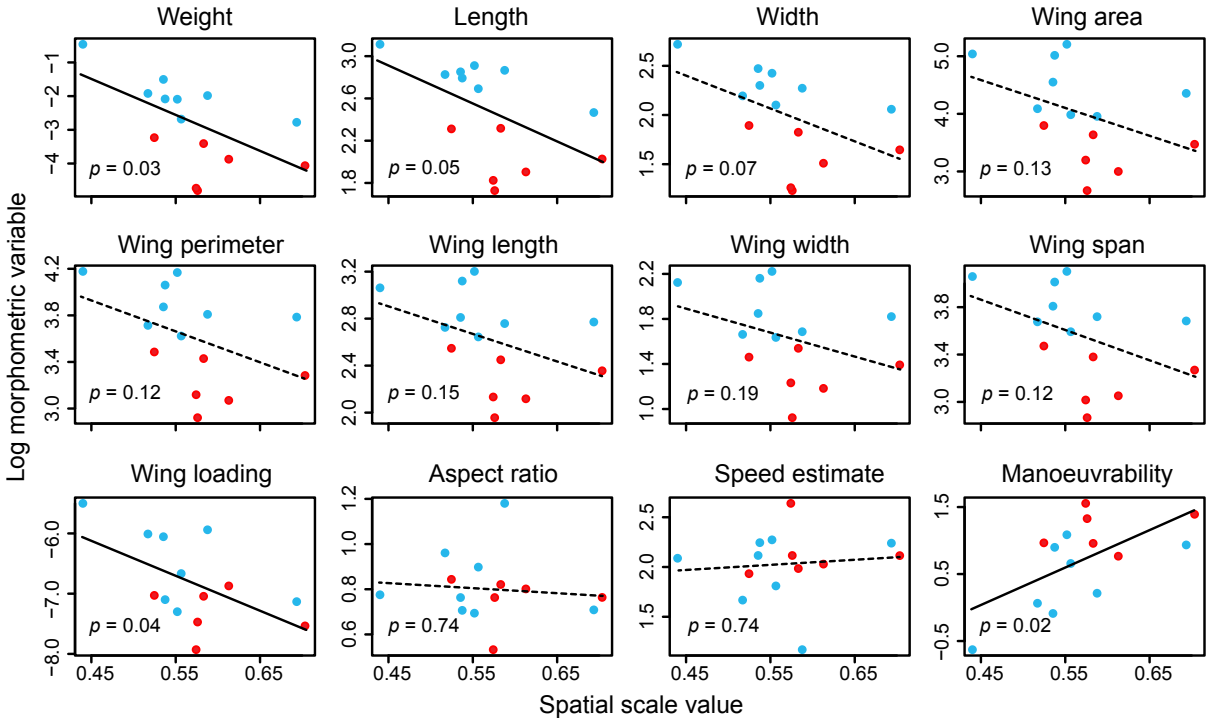


Figure 4.7. Morphometric variables regressed against 'spatial scale values', taken as the weighted means of adjusted R^2 values. All morphometric variables are log-transformed. Slopes from linear regressions are overlaid on each plot and p-values presented. Significant slopes have solid lines and non-significant slopes dashed lines. Species belonging to the large group are in green, and small species in red.

1.23, df = 13, $p = 0.24$, Fig. 4.6b). There were significant negative correlations between spatial scale values and body weight, body length and wing loading, and a significant positive correlation with manoeuvrability (Fig. 4.7).

4.4.2 Variation partitioning

After forward selection between one and seven DBMEMs were selected for each habitat. DBMEMs 1–8 were assigned as medium-scale, and DBMEMs 14–34 as fine scale. No fine-scale DBMEMs were selected in *Eucalyptus* plantations and so we did not carry out variation partitioning at the fine-scale for this habitat. Global models explained 24–42% of variation in community composition (Fig. 4.8). The relative importance of drivers between global models and between submodels varied depending on habitat and morphometric group. Environmental characteristics alone (green circles) played only a small, insignificant part in structuring dung beetle communities, explaining between 0–6%

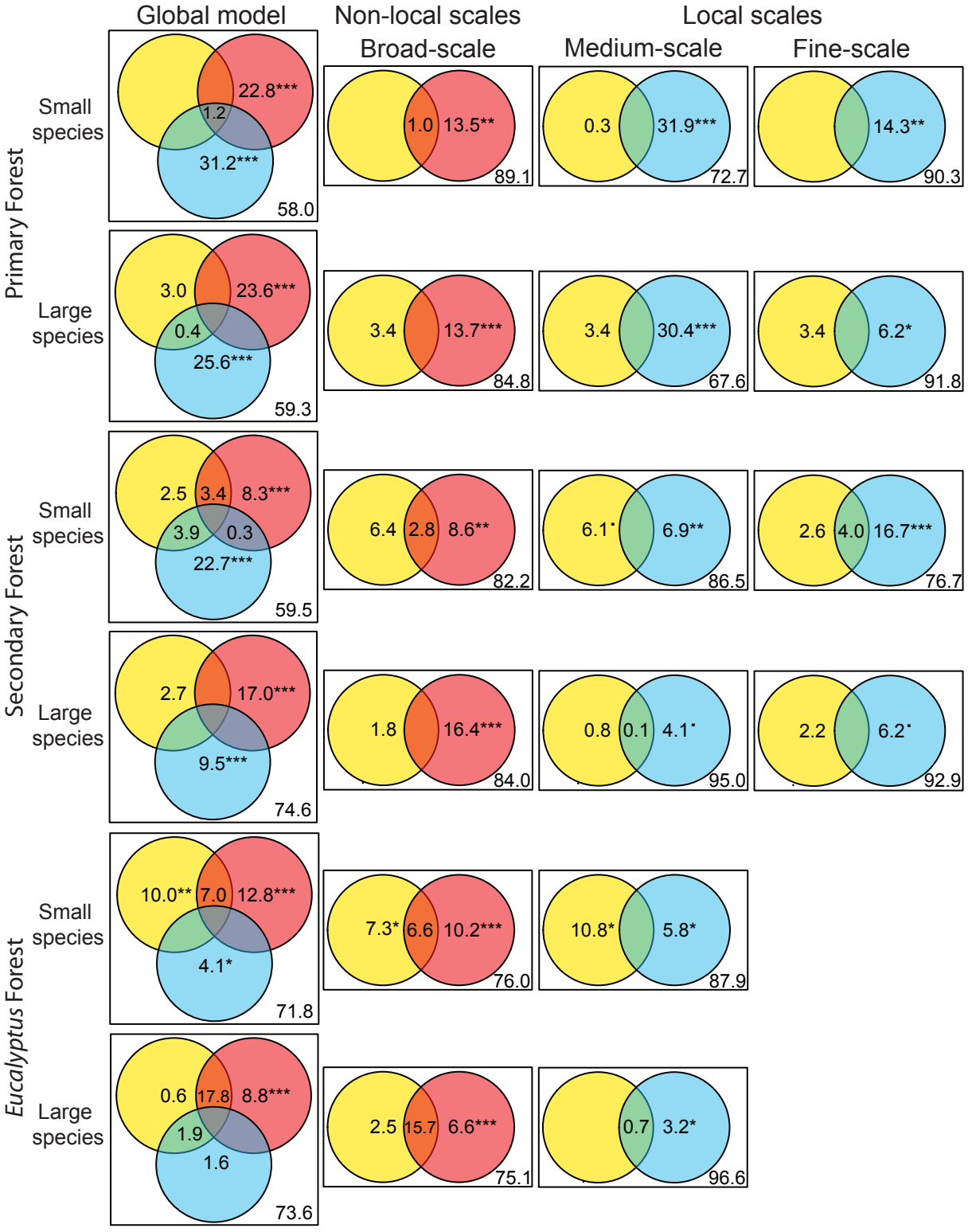


Figure 4.8. Relative influence of environmental variables (green), non-local space (red) and local space (blue) on dung beetle communities in primary, secondary and *Eucalyptus* forest. Global models were further partitioned into non-local broad-scale variation (linear trends greater than the extent of our sampling extent), and two local scales: medium-scale and fine-scale. Dung beetle communities were separated into two morphometric groups, small species and large species that differed in the spatial scale that their populations were structured. Numbers indicate the percentage variation explained. Numbers within boxes is the percentage residual variation. Significance of pure fractions: *** $p \leq 0.005$; ** $p \leq 0.01$; * $p \leq 0.05$; • $p \leq 0.1$. Significance of overlapping fractions cannot be tested

of variation, except for small species in *Eucalyptus* forest where environmental variables were significant, contributing up to 11%. Local space contributed higher percentages of explained variation (blue circles; 23–31%) than non-local space (red circles; 8–24%) in primary forest and for small species in secondary forest, whereas the opposite was true in *Eucalyptus* forest and large species in secondary forest (local space = 2–10%; non-local space = 9–17%).

4.5 Discussion

The relative contributions of variables were dependent upon habitat, scale and dung beetle morphology. In general, space was much more important than environment in structuring dung beetle communities, in line with previous studies (Louzada et al., 2010). Furthermore, local-scale variation (medium- and fine-scale) generally explained greater amounts of variation than non-local (broad-scale) variation. When local-scale variation was further decomposed, positive spatial autocorrelation at medium distances explained more variation than negative spatial autocorrelation at small distances. This is a common occurrence in variation partitioning (e.g. Laliberté et al., 2009) and is most likely down to unmeasured variables and biotic interactions at fine scales, such as the distribution of natural dung resources, competition and random dispersal. Apart from these general patterns, there were also important differences between habitats and the morphometric trait groups.

4.5.1 Inter-habitat differences

There were clear distinctions in the relative contributions of drivers in primary and secondary forest than in *Eucalyptus* forest. In the global models, local-scale processes were dominant in primary and secondary forest, however the opposite was true for *Eucalyptus* communities, where only a very small percentage of variation was attributable to local processes. One possible explanation is due to the larger proportion of generalist species and the homogenised nature of the habitat (in vegetation composition rather than structure, which varied widely between points; Fig. 4.4). In all likelihood, the generalist species

found in exotic plantations, which are adaptable to changes in environmental conditions, are responding to broad-scale processes and environmental gradients that we did not account for in our study. These generalist species are also likely to have high dispersal capabilities (Kotze and O'Hara, 2003), and so be less structured by fine-scale biotic interactions such as interspecific competition. In *Eucalyptus* there was also a large combined effect of broad-scale space and environment. This is due to induced spatial variation, where the spatial structure of environmental variables is similar to the spatial structure of the community (Borcard et al., 2004), and is most likely due to linear trends in soil composition.

4.5.2 Differences between morphometric groups

Results between morphometric groups were similar, with a few exceptions. Although the variation explained by environmental variables was low there were subtle differences between the two morphometric groups. In primary forest, environment explained some, although an insignificant amount, of variation in large dung beetle communities at all spatial scales (3%) but virtually none of the variation in small species (0–0.3%). However, in secondary forest, environment explained a larger amount of variation in the small dung beetle community (3–6%). Environmental characteristics may affect the ability of a dung beetle to occupy a habitat in several ways. First, different species may favour areas with different soil composition for breeding purposes (Doube, 1983, 1991). Canopy cover can also affect soil characteristics, such as soil moisture content and hardness that have consequences for larval survival (Sowig, 1995) and excavation (Doube, 1991). An open canopy may also lead to hotter, drier conditions that rapidly dessicates dung so that it becomes unusable to some species. A high understory density may favour species with high manoeuvrability, whereas species with fast flight may favour more open areas. Finally, vegetation composition and structure may affect mammal richness, which in turn is correlated with dung beetle richness (Andresen and Laurance, 2007).

The environmental variables in secondary forest differed from primary forest in a number

of aspects (Fig. 4.4). Although soil composition and canopy cover, which may affect soil characteristics, were similar, canopy height was greater in primary forest whereas understory vegetation was denser in secondary forest. Understory density is unlikely to be a major driver of spatial structure in the populations of small species, which have high manoeuvrability, however, both these structural variables may be predictors of mammal diversity. In the study area secondary forests hold a similar abundance of mammals as primary forest, but with increased representation of herbivorous ungulates and reduced primate diversity (Parry et al., 2007). If changes in the mammal composition results in changes in the spatial distributions of dung then this may have important consequences for the spatial distribution of dung beetles, and each species group may be affected differently. Small species forage over small areas and so are likely to occur in high densities where there were previously large aggregations of dung. Large dung beetle species, however, forage over larger distances, and so are likely to disperse further from (and therefore be more likely to be trapped far from) these aggregated areas. If mammal distribution correlates with the spatial variation in our environmental variables then the subsequent variation in small dung beetle communities will be attributed to environment. If, however, the mammal community responds to different processes then this variation will be attributed to space or residual variation.

This argument is strengthened in that there was more variation at fine-scales in the small species group in secondary forest than in all other submodels (23% compared to 7–9%). Fine-scale processes in multi-scale variation partitioning are often considered to involve inter- and intra-specific competition (Dray et al., 2006), which may be particularly important in structuring small species populations (Hanski and Cambefort, 1991). As dung is an ephemeral and widely-spaced resource, competition for dung is known to be extremely high amongst dung beetles (Horgan, 2001, Horgan and Fuentes, 2005). Large species are able to outcompete small species (Horgan and Fuentes, 2005) but require larger dung sources to reproduce (Doube, 1990; Horgan, 2001). In contrast, small species may specialise on smaller dung patches with reduced competition (Errouissi et al., 2004, Peck and Howden, 1984), and are known to visit several dung patches before reproducing

in a patch that has a sufficiently low density of dung beetles already present (Horgan, 2005). If dung resources are more aggregated in secondary forests this may point to biotic interactions, such as competition at dung, being a major driver behind the β-diversity of small species, but not large species, in these degraded habitats.

4.5.3 Limitations with the study

Partitioning the relative importance of spatial versus environmental drivers is dependent upon collecting information on appropriate environmental variables. Although the spatial distribution of dung may be important, it was, unfortunately, not possible for us to collect data on natural dung deposition in our study. Furthermore, the relatively small amount of variation in environmental drivers in structuring dung beetle communities could be due to the environmental variables measured within our study. Doubtless there will be unmeasured variables in our data which play significant roles in dung beetle breeding and survival and if these correlated with the spatial structure of our sampling points then the variation would have been attributed to space. Dung beetles species also vary in their thermoregulatory tolerances (Chown, 2001, Chown and Klok, 2011) and so they may respond strongly to microclimatic variation, such as temperature (Lobo et al., 2002, Lobo and Martín-Piera, 2002), which we were not able to measure. Other, more changeable variables may also be important, such as soil hardness (Doube, 1991) and moisture content (Sowig, 1995). Therefore, we must be careful in making firm conclusions on the importance of niche versus neutral processes governing the β-diversity of our dung beetle communities (Anderson et al., 2011, Dray et al., 2012). We feel, however, that the multi-scale approach used in this study, does afford us an idea of the scales at which the communities were structured, and that these scales vary between habitat and between morphological trait groups.

4.5.4 Morphological traits, spatial scale structuring, and the competition for resources

The morphometric analyses suggest that there were two distinct groups within our dung beetle community that could be separated by flight ability traits: small species and large species. These groups adopt opposing foraging strategies due to their morphological limitations, and so are likely to differ in their foraging ranges. This was corroborated by the spatial scales at which the communities of the two groups were structured in variation partitioning.

First are large species with high wing loading that favours foraging in continuous, active flight. These large species are highly competitive at dung resources, but require large dung patches to breed and so may forage over large distances. As such, their community structure is determined by medium- and broad-scale processes. By contrast, small species have low wing loading and high manoeuvrability. These species adopt a perch-and-wait strategy, foraging over small areas, but are less competitive and may need to visit several dung patches before breeding. The structures of their communities are determined to a greater extent by fine-scale inter- and intra-specific competition at dung patches.

However, the scales and identities of the drivers of spatial turnover in community composition are also dependent upon habitat. Primary forest communities were largely structured at local scales, and it seems that biotic interactions may play an important role in driving distribution patterns in these communities. By contrast, highly degraded or homogenised habitats, such as *Eucalyptus* plantations, may favour a community that is structured at large spatial scales where competition is relatively unimportant. This suggests that not only may habitat change result in large changes in community composition, but also that it may alter the processes, and the scales of those processes, that are driving patterns of community composition.

Chapter 5

Is spatial turnover greater at forest edges? A case study of Amazonian dung beetles

Charles J. Marsh & Robert M. Ewers

Prepared for submission to Biotropica

5.1 Abstract

A substantial quantity of rainforest edges are created every year through deforestation and forest fragmentation. However, we have little knowledge of the impacts of edges on spatial patterns of species turnover, β-diversity. We sampled dung beetles in the wet and dry season using baited pitfall traps in a quasi-experimental landscape in the north-east Brazilian Amazon. Using a sampling design based upon a fractal series of equilateral triangles we sampled two types of edges (primary-secondary forest and primary-*Eucalyptus* forest) and three control sites located in primary, secondary and *Eucalyptus* forest. We measured species turnover both between communities across the forest-matrix border, and within communities at up to 1 km from the forest edge. We found no relationship between β-diversity and distance to edge at the younger primary-Eucalyptus forest edge, however bray-Curtis dissimilarity-distance slopes were steeper at the primary-secondary forest edge than in habitat interiors. Regression slopes of dissimilarity-distance slopes was shallower from the edge-primary forest interior than the edge-secondary forest interior, suggesting that edge effects were still influencing β-diversity at 1 km in to the primary forest. This indicates that for a significant proportion of Amazonian communities the underlying processes determining diversity may be being affected by deforestation.

5.2 Introduction

The rate and spatial configuration of deforestation are causing a rapid increase in the quantity of 'core' habitat being converted to 'edge' habitat in the Amazon (Ewers and Didham, 2006b). It is estimated that some 70,000 km of new forest edge per year is created every year, and by 2002 over half of a large proportion of the Brazilian Amazon was within 2 km of the forest edge (Broadbent et al., 2008), resulting in a significant increase in the quantity of forest that is exposed to the ecological influences of edge effects.

Edge effects incorporate a wide range of well-established biotic and abiotic changes that occur in forest at close proximity to the forest-matrix boundary (Laurance et al., 2002, Murcia, 1995) that may act synergistically, resulting in cumulative impacts on diversity (Laurance et al., 2011, Malcolm, 1994). As the forest is exposed to the matrix habitat, altered microclimatic fluxes, including light, heat, moisture and wind turbulence (Kapos, 1989, Weathers et al., 2001) affect the structural responses of the forest bordering edges (Harper et al., 2005) leading to hotter, drier conditions than the interior (Chen et al., 1999), an increase in leaf-litter depth and decomposition (Didham and Lawton, 1999), and an increase in surface fire susceptibility (Cochrane, 2001). These structural responses cause a plethora of community-level impacts, such as alterations to invertebrate community structure (Didham et al., 1998a, Margules et al., 1994), tree composition (Laurance et al., 2006) and altered trophic interactions (Crooks and Soule, 1999, Hartley and Hunter, 1998, Terborgh et al., 2001). Although microclimatic variables typically reach normal levels within a few hundred metres (Laurance et al., 2002), the changes on communities may be much more pervasive, penetrating over a kilometre in to the forest interior (Curran et al., 1999, Ewers and Didham, 2008, Laurance, 2000).

The impacts of edge effects on patterns of diversity have been well studied (Ries et al., 2004). Species richness at the local scale, α-diversity, may vary greatly across a forest-matrix border, and proximity to edges may have a negative or positive impact on species

richness (Ries et al., 2004). Often we may see an increase in species richness at the edge as the matrix community mixes with the forest community (e.g. Ewers et al., 2007). However α-diversity may comprise only a small component of overall diversity, γ-diversity (Tylianakis et al., 2006a), especially in tropical ecosystems that are characterised by high β- and γ-diversity. However, relatively few studies explicitly address patterns of turnover or the processes that shape those patterns.

Typically, studies investigating the extent and magnitude of edge effects sample across the edge using transects running perpendicular to the border. As we travel from the forest interior across the edge and into the matrix habitat, we expect species characteristic of the forest interior to be replaced by species adapted to the matrix habitat. As a consequence, there may be an almost complete species turnover across the forest edge as the community in one habitat is replaced by the community in another (Spector and Ayzama, 2003), and as such the community becomes more similar to the forest interior community with distance into the matrix interior (Dangerfield et al., 2003, Ewers and Didham, 2006a).

However, very few studies have investigated the magnitude to which β-diversity differs within, rather than among, communities located at different distances from a forest edge. Thus, the question arises whether edge effects (and proximity to edges) *per se* impact rates of spatial turnover. Quantifying this variation in β-diversity requires a different sampling design, and we must replace transects that run perpendicular to the edge with transects that run parallel to the edge. Studies that have implemented such designs have found some evidence that β-diversity may be higher along the edges of forest than the interior (Ewers and Didham 2008, Gabriel et al. 2006, but see Duraes et al. 2005).

We would implicitly expect higher β-diversity along forest edges for two reasons. First, as the forest community is replaced by the matrix community, we would expect a greater species turnover across the habitat boundary, where the change in habitat traits is most pronounced. Thus, since the replacement of forest species by matrix species is unlikely to

be uniform along the length of the boundary, communities will likely differ to a greater extent along the boundary compared to forest or matrix interiors. Second, ecological processes at forest edges can show hyperdynamism (Laurance, 2002), exhibiting increased frequencies or amplitudes of their dynamics, leading to persistent, increased ecological instability (Wang and Malanson, 2008). This hyperdynamism may also lead to greater fluctuations in populations and community composition (Laurance et al., 2011), and thus greater turnover within edge communities.

If β-diversity is higher at forest edges, we would also expect this difference to be more pronounced where the matrix habitat is more dissimilar to the original forest. Firstly, the forest in close proximity to the edge may be more exposed to variations in microclimate, and thus edge effects will be more marked, and secondly there is likely to be a greater dissimilarity between the forest and matrix communities and so the turnover across the edge will be larger.

This study seeks to address two hypotheses: (1) the spatial turnover of species within communities along the forest edge will be higher compared to spatial turnover within communities of the forest interior; and (2) differences in species turnover will be greater where the structure of the matrix differs more strongly from the structure of the forest. To investigate these hypotheses we selected dung beetles (Coleoptera: Scarabaeinae) as effective and efficient indicator taxa (Gardner et al., 2008a, Spector, 2006) that fulfil a number of important ecological roles (Nichols et al., 2008), including nutrient cycling (Wu et al., 2011, Yamada et al., 2007), parasite suppression, soil aeration and perturbation, and seed dispersal and germination (Andresen, 2003). Dung beetles are highly sensitive to habitat gradients, fragmentation and proximity to edges (Davis et al., 2001, Filgueiras et al., 2011, Klein, 1989, Larsen et al., 2008, Spector and Ayzama, 2003) and, unusually for a tropical insect taxon, are well characterised and taxonomically well-determined for our study area (Gardner et al., 2008b). We sampled dung beetles in the dry and wet seasons across two edge types, a primary-secondary forest edge and a primary-*Eucalyptus* forest edge. By replicating 1 km transects at different distances parallel to the edge we

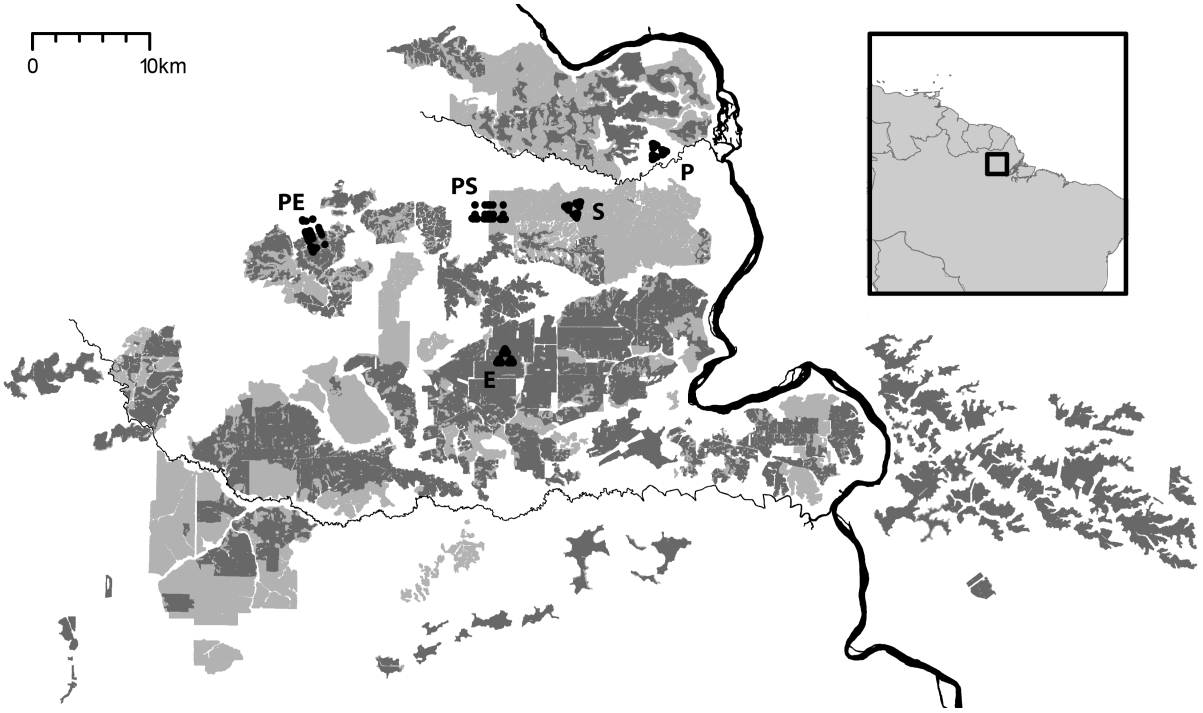


Figure 5.1. Map of the Jari forestry project study area. White areas are largely undisturbed primary forest, light grey areas are secondary forest and dark grey areas *Eucalyptus* plantations as of 2011. Black points indicate sampling points located in the five sampling locations: a control located in *Eucalyptus* (E), secondary (S) and primary forest (P); a primary-secondary forest edge (PS); and a primary-*Eucalyptus* forest edge (PE).

were able to model changes in the dissimilarity-distance decay within communities from the interior of primary forest across the forest edge in to the interior of the matrix habitat.

5.3 Methods

5.3.1 Study Area

The study was carried out at the Jari forestry project, an ongoing 50 year old pulp plantation located in the north-east Amazon in Pará, Brazil (00°27′00” − 01°30′00”S, 51°40′00” − 53°20′00”W), which provides a large-scale quasi-experimental landscape that has been previously well-studied (Barlow et al., 2007a). The project consists of a 1.7 Mha landholding, of which around 65,000 ha is *Eucalyptus* plantation and 45,000 ha cleared land and secondary forest as of 2011 (Fig. 5.1), the rest being largely undisturbed primary forest with occasional settlements (see Barlow et al., 2007b, for greater detail).

We sampled at five sites: one control site each in the interior of *Eucalyptus*, secondary and primary forest; and two edge sites: a primary-*Eucalyptus* forest edge and a primary-secondary forest edge. Sites were located sufficiently far apart so that points between sites should be independent of spatial autocorrelation effects (mean distance between different sites = 16.6 km; range = 5.2–31.6 km, Koenig 1999).

Control sites were located within the deep interior of each habitat, and all points were >0.95 km from the nearest border with an adjacent habitat. Sites within secondary forest were located within a large continuous block of 17–25 year old regenerating forest. Sites within *Eucalyptus* plantations were 2–3 years of age from last planting at the start of sampling (plantations are typically cut on a 4–5 year cycle). Edge sites were located on straight borders between primary forest and the adjacent matrix. As multiple edges may act synergistically (Laurance et al., 2011, Malcolm, 1994), the edges selected were chosen as they extended at least 1 km in both directions beyond each end of the edge transect.

5.3.2 Sampling design

Previous research found that classical sampling designs may be unsuitable for quantifying β-diversity (Marsh and Ewers, 2012). Therefore we sampled communities using a sampling pattern based upon a fractal series of equilateral triangles created explicitly for the investigation of β-diversity. The design allowed us to sample broad spatial scales while simultaneously maintaining fine scale data at all locations (Ewers et al., 2011). In simulations this design was found to provide more accurate estimates of β-diversity across all spatial scales than classical designs of equivalent sampling effort (Marsh and Ewers, 2012).

For a sample design of one order, three points are located on the apices of an equilateral triangle (Fig. 5.2a). From these three points we can generate three estimates of community turnover, and so also obtain a measure of the variance around that estimate. For two spatial scales, a 2nd order triangle is created, with three 1st order triangles, and thus nine

sampling points located on the apices. For three spatial scales, three 2nd order triangles and nine 1st order triangles are located on the apices, and so on. This was repeated for four spatial scales, with triangles of side lengths of $10^{1.5}, 10^{2}, 10^{2.5}$ and 10^{3} m. At the three control sites we reduced the sampling effort required by replacing two of the 1st

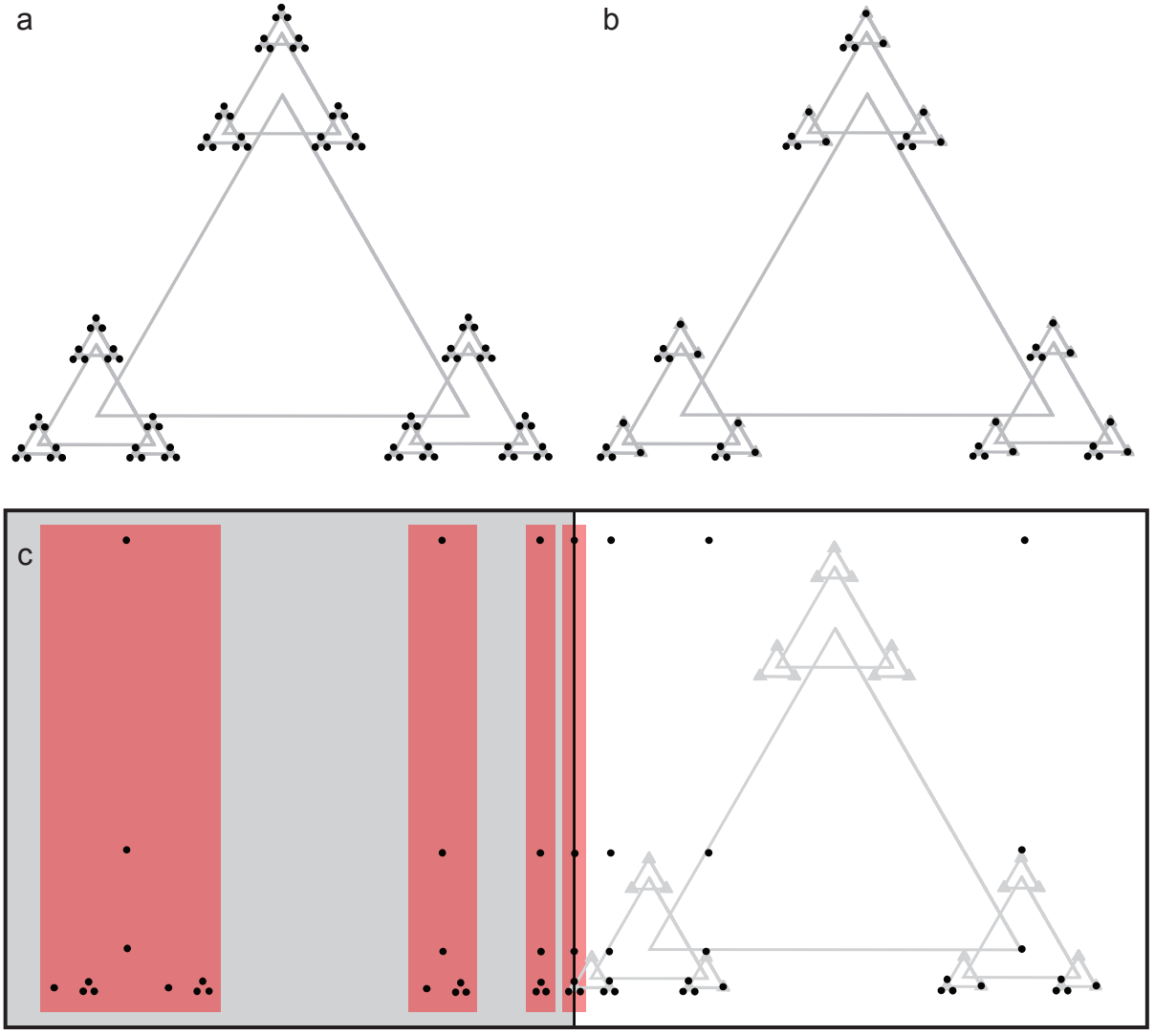


Figure 5.2. Sampling designs based upon a series of triangle fractals. Black points represent sampling locations. (a) A full sampling design with a sampling point located at each apex of every 1st order triangle, replicated at four spatial scales. (b) The compromise subsampling design used at control sites that reduces the sampling effort whilst maintaining the ability to estimate β-diversity at all spatial scales. (c) The sampling design used at forest edges where the black line represents the border between one habitat (grey) and another (white). The triangle fractal scheme is overlaid on one half to demonstrate how the same spatial scales are applied to edge sampling as control sampling. By linearising the fractal design we can create seven 'transects' (red boxes) at set distances from the edge.

order triangles with a single sampling point (Fig. 5.2b). In this way we were able to significantly reduce sampling effort with little loss in statistical rigour (Marsh and Ewers, 2012).

To model β-diversity within communities at set distances from the edge, we require transects running parallel to the edge. At edge sites we achieved this by linearising the edge of the control subsampling design to allow it to be transposed across the forest border (Fig. 5.2c). Thus the edge scheme may be considered as seven 'transects' running parallel to the border, whilst still maintaining the ability to estimate β-diversity at the smallest spatial scale. The distances between points at each spatial scale, and the distances of each 'transect' from the edge were equivocal to the control design to allow direct comparisons of spatial patterns of turnover. This allowed us to estimate β-diversity across the same four spatial scales as the control sites ($10^{1.5}, 10^2, 10^{2.5}$ and 10^3 m) and at four distances away from the border ($10^0, 10^2, 10^{2.5}$ and 10^3 m) and into both the forest and matrix interior.

5.3.3 Sampling

We sampled dung beetles using baited pitfalls flush with the ground (20 cm width, 15 cm depth), containing water with the addition of salt and detergent, that has been previously successful in sampling dung beetles in the study area (Gardner et al., 2008b). Bait was a 20 g mix of pig and human dung in a 90:10 ratio that was found to be an optimal compromise between effectiveness and bait availability within the study area (see Chapter 3). The bait was suspended below a protective cover directly above the pitfall. Traps were operated over a 4 day period, re-baiting after 2 days and contents were collected after 2 and 4 days.

One trap was placed at each sampling point (45 at control sites, 54 at edge site). Five points were removed from the primary-*Eucalyptus* forest edge site as they were located

within a manioc plantation. Sampling was carried out once in the early dry season (Jul–Oct 2010), and then repeated in the early wet season (Feb–Apr 2011). Specimens were sorted and oven dried at the study site, then identified to species level and deposited at Universidade Federal de Lavras (UFLA). Where species names were unknown we identified individuals to morphospecies using the classifications of Vaz-de-Mello and Gardner (2009, unpublished). For all analyses we pooled species collected during all sampling occasions for each trap.

5.3.4 Analyses

We estimated levels of β-diversity by modelling the dissimilarity-distance decay typical of natural communities which was found to be relatively robust to differences in sample size (Marsh and Ewers, 2012) and should not be affected by the differences in effort between transects at different distances from the edge. We modelled dissimilarity-distance decay in two ways: between communities across the edge; and within communities at different distances from the edge. Modelling was carried out separately for the primary-secondary forest and the primary forest-*Eucalyptus* sites on untransformed abundance data. All analyses were carried out in program R version 2.13.1 (R Development Core Team, 2011).

For modelling across the edge, as the primary forest control was non-continuous with the primary forest at the edge sites and there was naturally high species turnover between the five sites, for each edge site we used the transect located furthest inside the primary forest interior (i.e. 1 km) as the 'reference' interior community. We estimated Bray-Curtis dissimilarity between all pairs of sampling points in the reference transect and sampling points in each distance class away from the forest edge into the forest interior (negative edge distance values) and away from the forest into the matrix (positive edge distance values). The 'background' level of turnover was estimated as the mean dissimilarity between all pairwise comparisons within the reference transect.

To determine if the dissimilarity-distance decay is steeper within communities at the forest

edge compared to communities of the forest interior, we followed three steps. First, we estimated the slope and intercept of a beta regression (Cribari-Neto and Zeileis, 2010) that fitted Bray-Curtis dissimilarity against $\log_{10}$-transformed distance, with the regression fitted separately within each edge distance class. Beta regression allows a regression analysis to be carried out where the dependent variable is proportional data and therefore bounded at 0 and 1. However, as beta regression cannot be carried out when data contains absolute values of 0 (all species shared and of equal abundance) and 1 (no shared species), these values were replaced with arbitrarily small values of 0.001 and 0.999 respectively. The analysis was repeated for each control site except that all pairwise comparisons were used. From these models we extracted two estimates, the slope and the predicted value for dissimilarity at a distance of 35 m. In effect this value is 'initial similarity' *sensu* (Soininen et al., 2007b), and represents the level of beta diversity at the finest scales. Using linear regression we modelled these estimates against distance from the forest edge. Both linear and quadratic models were tested and the best model determined through Akaikes Information Criterion (AIC, Akaike 1974). Third, we investigated if the edge effect on β-diversity, represented as the change in the slope of the dissimilarity-distance curve at different edge distances, differed among habitats by comparing the linear regression slopes from the edge to the habitat interiors

5.4 Results

We captured 11,126 individuals of 79 species from 1,746 trap-nights (Appendix D.1). Species accumulation curves (Appendix D.2) suggested that 77-84% of species were captured at each site (first-order jackknife index; Appendix D.3). There were discernible patterns of changes to the richness, structure and abundance of dung beetles communities across the primary -*Eucalyptus* forest edge (Appendix D.4). Rarefied species richness, standardised abundance and community evenness decreased across the edge in to *Eucalyptus*, whereas the proportion of singletons increased. There were no such patterns across the primary-secondary forest however, although rarefied richness showed some decline (Appendix D.5).

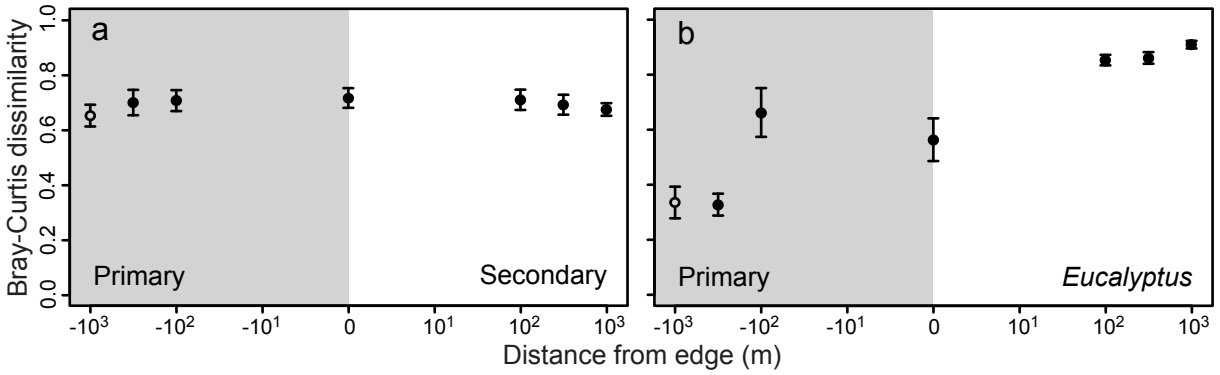


Figure 5.3. Mean ± 95% confidence interval of Bray-Curtis dissimilarity of all pairwise comparisons between communities sampled at 1 km inside the primary forest interior and at communities sampled at six distances from the forest edge both within primary forest (negative edge distances, shaded grey) and into the matrix (positive edge distances) for primary forest bordering (a) secondary forest, and (b) *Eucalyptus* forest. Open circles are the mean dissimilarity between all pairwise comparisons within communities at 1 km.

Similarly, at the primary-secondary forest edge, we found no significant change in community dissimilarity with the interior primary forest community across the forest edge (Fig. 5.3a) and pairwise Wilcox tests found no significant differences between distance classes. By contrast, at the primary-*Eucalyptus* edge there was a large turnover in community composition between the primary forest interior and those within the *Eucalyptus* (Fig. 5.3b). The interior *Eucalyptus* community showed the greatest dissimilarity with the interior primary forest community, and even the primary forest community 100 m from the edge was significantly different from β-diversity within the interior. Furthermore, turnover within the primary forest interior community bordering secondary forest was significantly higher than the primary forest bordering *Eucalyptus* (Fig. 5.3 - open circles; one-way ANOVA: $F = 61.78, \mathrm{df} = 1, 14, p < 0.005$).

We found evidence for elevated β-diversity within communities at the primary-secondary edge but not at the primary-*Eucalyptus* edge (Fig. 5.4). At the primary-secondary edge, the slopes of dissimilarity-distance curves were significantly higher within edge communities than communities in the primary or secondary forest interiors (Fig. 5.4a). This difference was more pronounced on the secondary forest side of the edge than the primary forest side with steeper dissimilarity-distance slopes in the secondary than primary

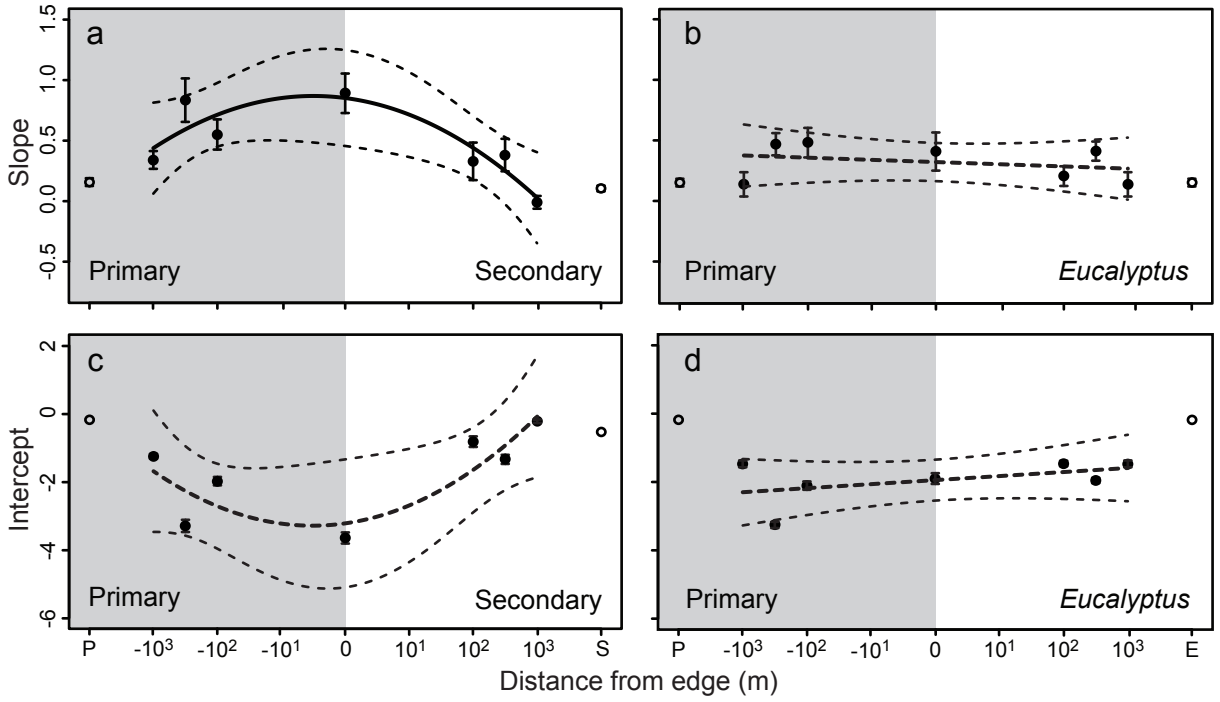


Figure 5.4. Slope (a, b) and intercept (c, d) ± se estimates of dissimilarity-distance curves (closed circles) estimated through beta regression at seven distances across the forest edge. Dissimilarity-distance was estimated in the primary forest (negative values, shaded grey) and the matrix habitat (positive values) for two edges, one of primary forest bordering secondary forest (a, c) and the other of primary forest bordering *Eucalyptus* (b, d). Open circles are the dissimilarity-distance slope estimates calculated from control sites far from habitat edges (>0.95 km), and are presented for comparison but were not used in estimating best fit lines. Thin, dashed lines are the 95% confidence intervals of the best fit lines. Heavy, dashed lines represent insignificant best fit lines.

habitat interiors at equivalent distances from the habitat edge (Fig. 5.5a; primary forest slope: slope = −0.14, se = 0.10, $p = 0.31$; secondary forest slope: slope = −0.27, se = 0.06, $p = 0.04$), although differences between slopes were insignificant. By contrast, dissimilarity-distance slopes did not vary across the primary-*Eucalyptus* forest edge (Fig. 5.4b) and neither slopes from the edge in to the interiors were significant (Fig. 5.5b; primary forest slope: slope = −0.05, se = 0.08, $p = 0.59$; *Eucalyptus* forest slope: slope = −0.08, se = 0.07, $p = 0.39$). There were no significant trends in the intercepts of the slopes, although patterns followed a mirror image of the trends in slopes (Fig. 5.4c, d).

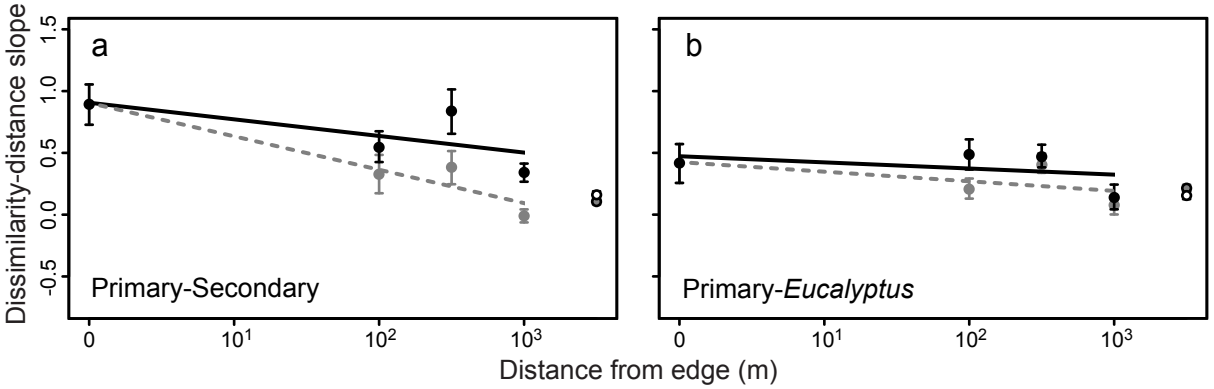


Figure 5.5. Slope ± s.e. estimates of the dissimilarity-distance curves from habitat edges into habitat interior for primary forest (black circles; black lines) and matrix habitat (grey circles; dashed, grey lines) for primary forest bordering (a) secondary, and (b) *Eucalyptus* forest. Open circles are the dissimilarity-distance slope estimates calculated from control sites far from habitat edges (>0.95 km); (white = primary forest, grey = matrix habitat), and are presented for comparison but were not used in estimating best fit lines.

5.5 Discussion

Anthropogenic edges provide a sharp boundary between a forest and matrix habitat. Species respond to the changes in the habitat structure and microclimate as we pass from the matrix to the forest, resulting in changes to the structure and composition of communities. Dung beetles have been found to be highly sensitive to these variations (Nichols et al., 2007), and we found clear differences in the patterns of richness and community structure across our two edge types. We found a large turnover between primary forest and *Eucalyptus* communities (Fig. 5.3), and this was reflected in decreases in species richness, abundance and community evenness across the edge in to *Eucalyptus* (Appendix D.4), as has been found previously in the study area (Gardner et al., 2008b). Edge communities more closely resembled primary forest communities in all metrics except for standardized abundance. There were, however, no such changes across the primary-secondary forest edge (Fig. 5.3, Appendix D.5), suggesting that communities in secondary forest more closely resembled primary forest communities than *Eucalyptus* communities did.

This concurs with previous investigations comparing communities between habitats both within the study area and globally. Secondary forests have been found to harbour a more complete subset of primary forest species than *Eucalyptus* in many taxa in the

region, including dung beetles (Barlow et al., 2007a), and dissimilarity was found to be higher between primary and *Eucalyptus* forest than primary and secondary forest in butterflies (Barlow et al., 2007c) and lizards (Gardner et al., 2007) but not in birds (Barlow et al., 2007b) and dung beetles (Gardner et al., 2008b). More generally, in a meta-analysis (Nichols et al., 2007) found that with increasing habitat modification dung beetle communities became less even, similarity with primary forest communities decreased and abundance and richness decreased.

Only two studies have specifically investigated edge effects on dung beetles (although limited to <240 m from the edge) and both similarly found that abundance, but not always richness, decreased towards the edge (Duraes et al., 2005, Feer, 2008). Feer (2008) investigated two edge types and they similarly found that the impact of edges on dung beetle abundance was more pronounced in forest bordering savannah than a road. They did not, however, estimate changes in within-community β-diversity across the edge.

Although abundance and richness were not greater at forest edges in our study, we did find elevated β-diversity at the primary-secondary forest border. Despite similar levels of β-diversity within the primary and secondary forest control sites, the decrease in β-diversity was greater from the edge to interior of primary forest than to the interior of secondary forest, such that levels of β-diversity 1 km in to the primary forest interior were still significantly higher than that in the primary forest control. This suggests a larger extent of edge effects on β-diversity (i.e. the influence of edge effects penetrates deeper) in primary forest, and that even at 1 km β-diversity was possibly still being affected by edge effects. These results suggest that whereas α-diversity may appear to recover to natural levels relatively close to the forest edge, this may be masking significant changes in the composition and spatial turnover of communities.

There was, however, no evidence for elevated β-diversity at the primary-*Eucalyptus* edge, although we predicted that any elevated β-diversity should be more pronounced due to the greater structural and floristic differences and larger between-habitat turnover

in community composition between the two habitats. A possible explanation for this discrepancy is due to the ages of the respective edges. The primary forest-*Eucalyptus* edge was much younger (2–3 years) than the primary-secondary forest edge (17–25 years old) and it may take several years or even decades for communities to attain a stable state post fragmentation (Laurance et al., 2011). For example, populations at newly created edges may see an initial hyper-abundance followed by a subsequent decline as populations become unsustainable (Hagan et al., 1996). Consequently, it may be that the dung beetle community at this edge had yet to attain equilibrium.

Furthermore the direction and structure of the edges may also influence the strength of edge effects (Kapos, 1989, Ries et al., 2004). A new edge that is structurally more open may exhibit stronger edge effects (Didham and Lawton, 1999) and the south-westerly facing primary-*Eucalyptus* edge may also experience stronger solar radiation than the easterly facing primary-secondary forest edge (Kapos, 1989). However, given the study sites position almost exactly on the equator these directional influences should be negligible.

5.5.1 Limitations of spatial scale and effort

We chose spatial scales that were appropriate for sampling the study taxon, covering an unusually large range of spatial scales for an investigation of edge effects (32–1440 m). The limited number of investigations in to dung beetle foraging distances found very limited dispersal, typically <50 m (Arellano et al., 2008, Larsen and Forsyth, 2005, Viljanen, 2009), although larger species with high wing-loading are suspected to cover greater distances (Larsen et al., 2008) and so our smallest scales should be fine enough to capture variation at the scales at which individuals interact. However, estimates of β-diversity within all three control habitats was low with a linear dissimilarity-distance decay unlike those typical of tropical communities across larger spatial scales (e.g. Condit et al., 2002) and so our largest scales may not be sufficient to capture broad-scale processes. While every increase in spatial scale covered typically increases sampling effort exponentially,

the use of cluster based sampling designs such as used in this study may prove useful for future studies analysing patterns at landscape level. However, this must also be accompanied with the caveat of finding edges of sufficient length, as well as achieving independence from adjacent habitat boundaries.

From our study it is difficult for us to ascertain the distance of edge influence due to the limited number of data points. Studies investigating edge effects typically focus effort within a few hundred metres of the edge within the range that microclimatic variables and habitat structure are still affected (Laurance et al., 2002), and thus where edge effects will be most pronounced. However, although edge influence on these physical factors extend only limited distances in to the forest interior, the impacts on populations and communities may be much more pervasive and pernicious. The few studies that have investigated deeper in to interior forest have found that communities may still be altered >1 km from the edge (Curran et al., 1999, Ewers and Didham, 2008, Laurance, 2000) and this may have serious impacts on predicting extinction rates and reserve designs (Broadbent et al., 2008, Ewers and Didham, 2008, Laurance, 2000). In this study we replicated these scales, but it was still not enough for levels of β-diversity to reach that of the interior for one of our sites and future studies should attempt to extend sampling several kilometres from the edge.

Chapter 6

General discussion

This thesis aimed to investigate a gap in our current knowledge of the effects of habitat fragmentation, namely the impact of habitat edges on β-diversity. I approached the subject systematically, first developing a sampling design that can accurately recover estimates of β-diversity across a broad range of scales. Second, I optimised methods for sampling the dung beetle community. Third I investigated the drivers of β-diversity, and linked them with morphological traits governing foraging strategy. Finally, I estimated turnover at two edge types and compared these estimates to those in habitat interiors. Here, I address several issues that arose from the study.

6.1 There was mixed evidence that β-diversity is elevated at forest edges

There was a clear, significant increase in β-diversity at the edge between primary and secondary forest, but no such increase at the primary-*Eucalyptus* edge where we predicted that differences would be more pronounced. By contrast, both abundance and richness decreased across the primary-*Eucalyptus* edge (Appendix D.4) but remained consistent across the primary-secondary edge (Appendix D.5) as we might expect due to the higher species richness of secondary forest compared to *Eucalyptus* forest (Appendix D.1).

In Chapter 4, I demonstrated that the relative influences of environmental and spatial drivers of β-diversity differ between habitats (Fig. 4.6). Patterns were similar between primary and secondary forest controls where local-scale space explained the most variation. This may indicate that intra- and inter-specific competition play an important role

in structuring dung beetle communities, and therefore the rates of spatial turnover, in these habitats. In *Eucalyptus* forest, however, non-local and environmental drivers had a much greater influence in determining patterns of abundance, suggesting that different processes, such as niche-partitioning are more important. Although these patterns were from the habitat interiors, if we extrapolate the results to our edges where the two communities meet, at the primary-secondary forest edge the two communities are responding to similar processes and at similar spatial scales, however at the primary-*Eucalyptus* edge, the two communities are responding to different processes at different spatial scales. The consequences for levels of turnover at the boundary between the two communities are unclear, but it may explain the differences between our two edge types.

As well as there being differences in the spatial structuring of the adjoining communities, there may also be physical differences between our two edges that may partially explain the differences I found. The magnitude and penetration of edge effects is dependent upon a collection of environmental characteristics (Harper et al., 2005, Ries et al., 2004), such as edge age (Didham and Lawton, 1999), 'softness' (Harper et al., 2005, Matlack, 1994) and direction (Kapos, 1989, Matlack, 1993), as well as the structural similarity between the two adjoining habitats (Harper et al., 2005). Of these, although the directions of the edges differed (east for the secondary forest edge, and south-east for the *Eucalyptus* edge) it is likely to have little consequence as our study site is situated almost on the equator. There were, however, significant differences in the ages between the edges. The primary-secondary forest edge was at an advanced stage of regeneration; the secondary forest adjoining the primary forest was left fallow 17–20 years previous. By contrast, the *Eucalyptus* was only 2–3 years old. This may have several consequences. It may take several years, if not decades for the communities at edges to stabilise after edge creation (Laurance et al., 2011) and so it may be that populations of dung beetles at the *Eucalyptus* edge were yet to attain equilibrium. Furthermore, the greater regeneration of the secondary forest will also lead to a 'softer' edge where the regenerated vegetation leaves the primary forest lest exposed to outside influences, although this should lead to less pronounced edge effects.

The major structural difference between the secondary and *Eucalyptus* forest in my study was in canopy cover, which was much lower in *Eucalyptus* forest (Appendix E.1). This could affect dung beetles in two ways. First, it may lead to the hotter, drier and more variable conditions that we found in *Eucalyptus* forest (Appendix E.2) which rapidly dessicate dung sources (Peck and Forsyth, 1982) and favour species with high thermal tolerances (Chown, 2001). Second, it may alter soil moisture content and hardness that may have consequences on species' dung burying ability (Doube, 1991) and larval survival (Sowig, 1995). Understory density was also particularly high at the primary-*Eucalyptus* forest edge (Appendix E.1) which may adversely affect large species with low manoeuvrability (Gill, 1991). There are also differences in the mammal communities between habitats (Barlow et al., 2007a, Parry et al., 2007); *Eucalyptus* plantations have a highly depauperate subset of the primary forest fauna, and this may have consequences for the dung beetle community (Andresen and Laurance, 2007).

These differences lead to a much greater dissimilarity between the primary and *Eucalyptus* forest communities (mean Bray-Curtis dissimilarity between all points = 0.98) than the primary and secondary forest communities (mean = 0.82). We would also expect the environmental conditions within *Eucalyptus* to favour a community of highly competitive generalists that are also likely to have high dispersal ability, and therefore be the first to arrive and colonise the new habitat after forest clearance. This is reflected in the results of the variation partitioning analyses, which revealed that non-neutral processes at large spatial scales played a dominant role in structuring *Eucalyptus* communities.

What remains unclear, however, is how differences in the drivers and scale of community composition translate to difference in β-diversity. For example, are communities that are structured at small scales likely to have greater turnover than communities that are structured at broad scales? And what are the consequences when two differently structured communities meet at habitat boundaries compared to when two similarly structured communities meet?

6.2 Current issues for studies quantifying β-diversity

In Chapter 2 I presented a sampling design upon a fractal series of equilateral triangles with the explicit aim of estimating β-diversity. Simulations found the sampling design to be more efficient at recovering accurate estimate of β-diversity than classical sampling designs, such as transects. However, the analyses also revealed insights in to the limitations of current analytical techniques in estimating β-diversity.

Our results show that estimates of β-diversity will vary with sampling effort, the spatial configuration of sampling points, the type of β-diversity being analysed and the spatial scale and range of spatial scales at which estimates are being generated. Therefore great care must be taken in comparing between studies that do not share exactly the sampling and analytical design of the other. In particular there was an alarming discrepancy between β estimates from the control and those of the classical sampling designs, such as transects.

Estimating directional turnover through distance-dissimilarity decay seemed relatively robust to sampling effort. Estimates of non-directional turnover through additive partitioning were, however, particularly sensitive to sample size. The issue lies in that the more extensive the sampling effort and number of sampling points the greater the estimate of γ-diversity. By contrast, these increases will not lead to an increase in the α-diversity estimate, which is the mean number of species per sampling point, only to an increase in the accuracy of the estimate. Therefore, as our estimate of γ increases, the estimate of β, calculated as the difference between γ and α, will likewise increase.

Things are further complicated when the β component is partitioned in to multiple spatial scales. A reduced sampling effort increases the proportion of diversity attributed to large-scale β. This overestimation will further be inflated by an inappropriate configuration of sampling points. Similarly, the variance around the distance-dissimilarity slopes increased with spatial scale, largely due to the reduction in the number of replications at these

scales. Therefore, particular care must be taken when making ecological inferences from these analyses, and it is perhaps inadvisable to carry out multi-scale additive partitioning unless data is extremely extensive, such as in remote-sensing studies.

Clearly there is much work still required to standardise β-diversity investigations. In particular, there remains much confusion about what we are trying to quantify when measuring β-diversity and what terminology to use. Although there have been numerous attempts to make sense of the bewildering array of metrics available to us (Anderson et al., 2011, Baselga, 2010, Gaston et al., 2007, Tuomisto, 2010a,b, Vellend, 2001) there is still a need for a clear and standardised terminology of what processes we are attempting to describe when we investigate β-diversity. The titles of these reviews sum up the current confusion - "A diversity of beta diversities: straightening up a concept gone awry" (Tuomisto, 2010a,b); "Navigating the multiple meanings of β-diversity: a roadmap for the practicing ecologist" (Anderson et al., 2011); "The scaling of spatial turnover: pruning the thicket" (Gaston et al., 2007) and this lack of clarity leads to studies purporting to be investigating the same thing (β-diversity), whilst actually investigating different, mutually exclusive processes.

Thus, the concept of β-diversity has come to encompass numerous different ecological processes and it would perhaps be more useful to separate these concepts into exclusive ideas. For example, using the terminology of Anderson et al. (2011) we could usefully abandon the term β-diversity, and instead consider 'directional' and 'non-directional' turnover. The former describes the spatial turnover in community composition (e.g. Nekola and White, 1999), which is determined by such processes as neutral versus niche processes, and dispersal and competition (Legendre et al., 2005). The second concept, however, does not address differences in communities across space, rather ideas of local-regional richness relationships and spatial subsetting (e.g. Gering and Crist, 2002, Lande, 1996). Including both in our analyses certainly strengthens the insights in to the processes structuring diversity, however it is confusing for them both to have the same terminology when they are clearly describing different phenomena.

In turn, many studies also need to be more precise and clear about what aspect of β-diversity they are investigating, and to take greater consideration about the effort, range, and configuration of sampling. I also strongly urge any study seeking to investigate patterns of diversity to consider the sampling design explicitly with β-diversity in mind, and not α- or γ-diversity which are both robust to differences in sampling design.

6.3 Further work and future directions

Clearly it is difficult to make generalisations from the small sample size in my study of only two edge types. Furthermore, the three habitats are all forest with differing degrees of anthropogenic influence. Although the *Eucalyptus* plantations present an extreme homogenised version of forest in many ways it remains structurally similar, particularly to secondary forest. The results from this thesis could further benefit both by replications of the same edge types, as well as repeating the study with different edge types.

In this thesis I have presented results with dung beetles, however I also repeated the sampling with ants and I am currently awaiting identification of the material. Using honey and sardine baited pitfalls I sampled both below-ground and at ground-level in the dry and wet seasons. I also developed a new baited pitfall design that allowed me to sample all 168 primary and secondary forest sites at canopy-level. As well as providing replication of the dung beetle data, to my knowledge there are no studies that have quantified turnover at multiple strata within the forest, and this raises interesting questions.

First, we may investigate turnover *between* communities at different strata, i.e. vertical turnover in species composition from below-ground to canopy-level. Second, we may investigate turnover *within* communities at different strata i.e. horizontal turnover at different levels within the forest. In particular, we might expect turnover to be higher in strata where dispersal is more limited. This work would greatly enhance our knowledge of patterns of tropical forest diversity, and how the hyper-richness of rainforest communities are maintained.

Appendix A: Supporting information for Chapter 2

A.1 R code for creating and sampling simulated communities

```
### Code for creating and sampling simulated communities (windows only)
#
# Model parameters (number of species, grid size, distribution probabilities
# etc) may be selected from the options or inputed directly by the user by
# editing the code.
#
# Users must provide a text file containing the coordinates of the sampling
# design.  This should be in the format of two columns (x and y) with headers.
#
# The final output is a presence-absence matrix of species (columns) at each
# sampling point (rows).
#
### Warning ###
# the code will only work in windows, although it can work on Macs etc if the
# user inputs all the parameters individually

wd<-choose.dir(getwd(),"Choose working directory")
setwd(wd)
spatial<-function(X,i,j) max(X[(i-1):(i+1),(j-1):(j+1)]==1)
library("tcltk")

### Choose the parameters for the landscape (grid size, number of species etc)
no_species<-tk_select.list(c(10,25,50,100,250),title="Select number of species
     \n ***WARNING*** large values may result in significant processing times")
no_runs<-tk_select.list(c(1,10,25,50,100),title="Select number of repeats
     \n ***WARNING*** large values may result in significant processing times")
range_grad<-tk_select.list(c(0,0.5,1,1.5,2,2.5,3),
     title="Select strength of environmental gradient")
grid.size<-t_select.list(c(25*25,50*50,100*100,250*250,500*500,1000*1000),
     title="Choose size of 'landscape' \n ***WARNING*** large values may result
     in significant processing times")
name.coords<-choose.files(default=wd,caption="Choose file with sampling
     coordinates",multi=FALSE)
coordinates<-read.table(name.coords,header=T)

### Choosing parameters for the species distributions

Mostly_rare_species<-rbeta(no_species,0.6,5)
Many_rare_species<-rbeta(no_species,1,4)
Normally_distributed<-rnorm(no_species,0.5,0.15)
Many_common_species<-rbeta(no_species,4,1)
Mostly_common_species<-rbeta(no_species,5,0.6)

No_response<-runif(no_species,0,0)
```

```
One<-runif(no_species,-0.5,0.5)
Two<-runif(no_species,-1,1)

prob_occur<-get(tk_select.list(c("Mostly_rare_species","Many_rare_species",
     "Normally_distributed","Many_common_species","Mostly_common_species"),
     title="Select Distribution of Probability of Occurence"))
envir_resp<-get(tk_select.list(c("No_response","One","Two"),
     title="Select Range of the Responses to the Environmental Gradient"))
dens_depend<-get(tk_select.list(c("No_response","One","Two"),
     title="Select Range of the Values for Density Dependency"))

### Choose Outputs

print_sp<-winDialog("yesno","Print species distributions on screen\n
     ***WARNING*** visualises each species distribution for 0.5secs")
save_sp<-winDialog("yesno","Save individual species distributions")

### Run simulation model

for (z in 1:no_runs){

   ########################
   ## create environmental gradient

   side<-sqrt(grid.size)
   gradient<-matrix(rep(0,((side+2)^2)),nrow=(side+2))
   px<-runif(1,-1,1)
   py<-runif(1,-1,1)
     for (a in 1:(side+2)){
       for (b in 1:(side+2)){
         gradient[a,b]<-(a*px)+(b*py)
       }
     }
   fac1<-range_grad/(max(gradient)-min(gradient))
     for (a in 1:(side+2)){
       for (b in 1:(side+2)){
         gradient[a,b]<-gradient[a,b]*fac1
       }
     }
   fac2<-(range_grad/2)-max(gradient)
     for (a in 1:(side+2)){
       for (b in 1:(side+2)){
         gradient[a,b]<-gradient[a,b]+fac2
       }
     }
```

```
######################
## create species matrices

for(i in 1:no_species){
  PO<-prob_occur[i]
  SA<-dens_depend[i]
  ER<-envir_resp[i]

  FPO<-random<-presence<-matrix(rep(0,((side+2)^2)),nrow=(side+2))
  f<-g<-rep(2:(side+1),each=side)
  xs<-sample(f)
  ys<-sample(g)
    for(a in 1:grid.size){
      correlation<-spatial(presence,xs[a],ys[a])
      FPO[xs[a],ys[a]]<-PO+(correlation*SA)+(gradient[xs[a],ys[a]]*ER)
      random[xs[a],ys[a]]<-runif(1,0,1)
      if(random[xs[a],ys[a]]<FPO[xs[a],ys[a]]) {presence[xs[a],ys[a]]<-1}
      if(random[xs[a],ys[a]]>FPO[xs[a],ys[a]]) {presence[xs[a],ys[a]]<-0}
    }

  f<-g<-rep(2:(side+1),each=side)
  xs<-sample(f)
  ys<-sample(g)
    for(a in 1:grid.size){
      correlation<-spatial(presence,xs[a],ys[a])
      FPO[xs[a],ys[a]]<-PO+(correlation*SA)+(gradient[xs[a],ys[a]]*ER)
      random[xs[a],ys[a]]<-runif(1,0,1)
      if(random[xs[a],ys[a]]<FPO[xs[a],ys[a]]) {presence[xs[a],ys[a]]<-1}
      if(random[xs[a],ys[a]]>FPO[xs[a],ys[a]]) {presence[xs[a],ys[a]]<-0}
    }
  presence<-presence[-1,-1]
  presence<-presence[ -(side+1),-(side+1)]
  name<-paste("sp",i,sep="")
  assign(name,presence)

  if(print_sp=="YES"){
    print(image(1:side,1:side,presence,col=c("white","red"),
       xlab="",ylab="",axes=F))
    box(col="black")
    Sys.sleep(0.5)
  }

  if(save_sp=="YES"){
    name<-paste("Species",i,".txt",sep="")
    write.table(presence,name,row.names=F,col.names=F)
  }
}
```

```
  ############################
  ### Creating site by species matrices


  PA<-present<-NA
  for(i in 1:no_species){
    for(a in 1:length(coordinates[,1])){
      species<-paste("sp",i,sep="")
      sp<-get(species)
      dim(sp)<-c(side,side)
      cell<-coordinates[a,]
      random<-runif(1,0,1)
      if(sp[cell[[1]],cell[[2]]]==1) (present[a]<-1)
      if(sp[cell[[1]],cell[[2]]]==0) (present[a]<-0)
    }
    PA<-cbind(PA,present)
    colnames(PA)[(i+1)]<-species
  }
  PA<-PA[,-1]
  file.name<-paste("Sampled_community_",z,".txt",sep="")
  write.table(PA,file.name,row.names=F,col.names=T)
}
```

Appendix B: Supporting information for Chapter 3

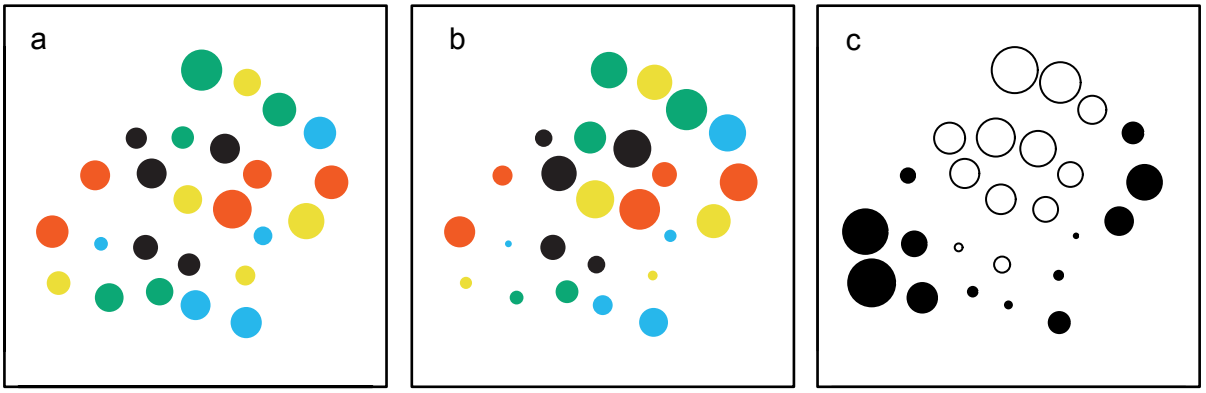
Table B.1. The number of individuals for each species captured by each bait type. Breeding strategy and diel activity is taken from Feer and Pincebourde (2005).

Species	Human	10%	50%	90%	Pig	Strategy	Activity
Ateuchus aff. *connexus*	5	3	8	19	9	Sm. tunneller	Diurnal
Ateuchus aff. *murrayi*	2	7	1	11	2	Sm. tunneller	Diurnal
Ateuchus irinus	15	32	35	64	2	Sm. tunneller	Diurnal
Ateuchus pauki	1					Sm. tunneller	Diurnal
Ateuchus sp. A			1	1		Sm. tunneller	Diurnal
Ateuchus sp. B				1		Sm. tunneller	Diurnal
Ateuchus sp. E	1	2	1	1	4	Sm. tunneller	Diurnal
Ateuchus sp. F		1				Sm. tunneller	Diurnal
Ateuchus sp. G	1	5		3	1	Sm. tunneller	Diurnal
Canthidium aff. *gertsaeckeri*	2	1	1	2	3	Sm. tunneller	Diurnal
Canthidium aff. *lentum*	3	12	2	5	3	Sm. tunneller	Diurnal
Canthidium sp. B		2	6		3	Sm. tunneller	Diurnal
Canthidium sp. D	1					Sm. tunneller	Diurnal
Canthidium sp. H	2			1		Sm. tunneller	Diurnal
Canthon bicolor	1	4		3	3	Sm. roller	Diurnal
Canthon quadriguttatus				2		Sm. roller	Diurnal
Canthon subhyalinus				1		Sm. roller	Diurnal
Canthon triangularis	89	97	3	53	43	Sm. roller	Diurnal
Coprophanaeus dardanus		1				Lg. tunneller	Crepuscular
Coprophanaeus jasius	1					Lg. tunneller	Crepuscular
Coprophanaeus lancifer	1	1				Lg. tunneller	Crepuscular
Deltochilum aff. *peruanum*	27	34	19	25	15	Lg. roller	Crepuscular
Deltochilum aff. *submetallicum*	32	13	21	11	14	Lg. roller	Crepuscular
Deltochilum carinatus	3	7	3	1	1	Lg. roller	Crepuscular
Deltochilum icarus	1			1		Lg. roller	Crepuscular
Deltochilum orbiculare	1					Lg. roller	Crepuscular
Dichotomius apicalis	2	3		4	1	Lg. tunneller	Nocturnal
Dichotomius boreus	1		1	1		Lg. tunneller	Nocturnal
Dichotomius latilobatus		3	3	3	3	Lg. tunneller	Nocturnal
Dichotomius lucasi	35	75	65	76	94	Lg. tunneller	Nocturnal
Dichotomius mamillatus			2			Lg. tunneller	Nocturnal
Dichotomius subaeneus	7	2	23	22	22	Lg. tunneller	Nocturnal
Dichotomius worontzowi	8	5	3	2	2	Lg. tunneller	Nocturnal
Eurysternus atroserucus	19	34	34	2	18	Dweller	Diurnal
Eurysternus balachowskyi	1	3	1	3		Dweller	Diurnal
Eurysternus caribaeus	37	9	61	34	41	Dweller	Diurnal
Eurysternus cayennensis		1				Dweller	Diurnal
Eurysternus foedus	5	17	27	21	8	Dweller	Diurnal
Eurysternus hamaticollis	1	3	1	1		Dweller	Diurnal
Eurysternus hypocryta	9	22	11	22	14	Dweller	Diurnal
Eurysternus strigulatus	4	21	23	29	24	Dweller	Diurnal
Eurysternus vastorium	2	4	1	8	1	Dweller	Diurnal

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Species	Human	10%	50%	90%	Pig	Breeding	Activity
Eurysternus ventricosus	3	5	5	9	1	Dweller	Diurnal
Onthophagus aff. *bidentatus*	13	33	8	3	14	Sm. tunneller	Nocturnal
Onthophagus aff. *clypeatus*	111	121	38	69	57	Sm. tunneller	Nocturnal
Onthophagus aff. *haemathopus*	6	8	2	4	2	Sm. tunneller	Nocturnal
Oxysternon durantoni	3	7	15	19	5	Lg. tunneller	Diurnal
Oxysternon festivum	13	28	12	28	9	Lg. tunneller	Diurnal
Phanaeus chalcomelas	5	7	9	11	2	Lg. tunneller	Diurnal
Sulcophanaeus faunus		1				Lg. tunneller	Diurnal
Uroxys sp. A	84	94	223	168	294	Sm. tunneller	Nocturnal
Uroxys sp. B					1	Sm. tunneller	Nocturnal
Uroxys sp. C	13	12	7	6	1	Sm. tunneller	Nocturnal

Figure B.2. Bubble plots of trap locations. Bubble size represents species richness (a) and number of individuals (b) for each trap. Colours represent dung type: human (blue), 10% pig (red), 50% pig (yellow), 90% pig (green), pig (black). There was significant spatial autocorrelation in abundance (c) but not for richness. Black bubbles represent positive spatial autocorrelation and white bubbles negative spatial autocorrelation.



Appendix C: Supporting information for Chapter 4

Figure C.1. Map of the Jari forestry project study area near the north-east coast of Brazil. White areas are largely undisturbed primary forest, light grey areas are secondary forest and dark grey areas Eucalyptus plantations as of 2011. Black points indicate sampling points located in three habitats: Eucalyptus plantation (E), secondary forest (S) and primary forest (P).

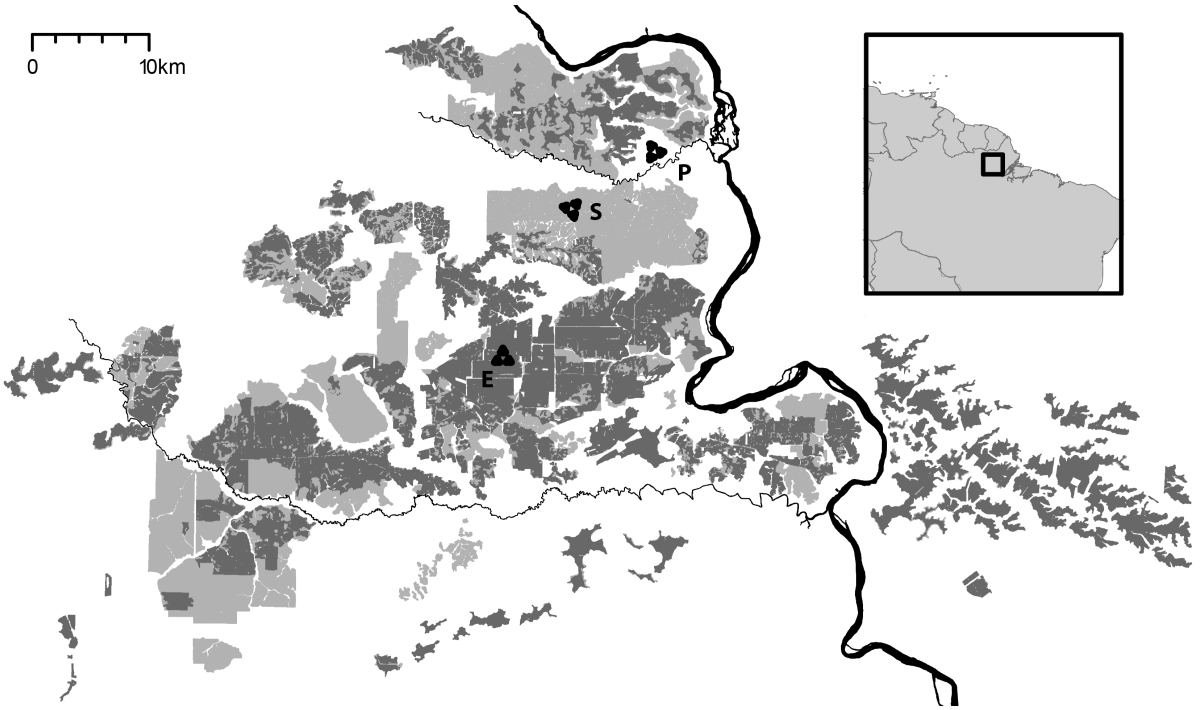


Table C.2. Pearsons correlations between log-transformed morphometric variables.

	Weight	Length	Width	Wing area	Wing perimeter	Wing length	Wing width
Weight							
Length	0.996						
Width	0.998	0.994					
Wing area	0.988	0.988	0.991				
Wing perimeter	0.968	0.965	0.955	0.938			
Wing length	0.975	0.97	0.96	0.945	0.986		
Wing width	0.992	0.993	0.993	0.993	0.945	0.955	
Wing span	0.954	0.957	0.939	0.925	0.98	0.979	0.936

Table C.3. Species abundances by site and if morphometric measurements were taken (Y = yes).

Species	Primary	Secondary	*Eucalyptus*	Total	Measured
Ateuchus aff. *connexus*	364	371	9	744	Y
Ateuchus aff. *murrayi*	42	317		359	Y
Ateuchus irinus	8			8	
Ateuchus sp. A	2	3	373	378	Y
Ateuchus sp. E	1			1	
Ateuchus sp. G	1			1	
Canthidium aff. *gerstaeckeri*	3	1		4	
Canthidium aff. *lentum*	4		143	147	Y
Canthidium sp. A	1			1	
Canthidium sp. B	3			3	Y
Canthidium sp. G	1			1	Y
Canthidium sp. H	4			4	Y
Canthidium sp. K	2			2	
Canthidium sp. L			3	3	
Canthidium sp. M	3			3	
Canthidium sp. N	1			1	
Canthon aff. *acutus*			56	56	
Canthon lituratus			48	48	
Canthon quadriguttatus	7			7	Y
Canthon scrutator			16	16	
Canthon simulans		1	545	546	
Canthon subhyalinus	10	5		15	
Canthon triangularis	58	145	2	205	Y
Coprophanaeus dardanus		3		3	Y
Coprophanaeus lancifer			1	1	Y
Deltochilum aff. *peruanum*	18	294		312	Y
Deltochilum aff. *submetallicum*	34	2		36	Y
Deltochilum carinatum	2			2	Y
Deltochilum icarus	1			1	Y
Deltochilum orbiculare	7	2		9	Y
Deltochilum sp. A	1			1	
Dichotomius aff. *lucasi*	114		4	118	Y
Dichotomius apicalis	113	5		118	Y
Dichotomius boreus	6		6	12	Y
Dichotomius carinatus		15		15	
Dichotomius latilobatus	3	6	29	38	Y
Dichotomius mamillatus	1	56		57	Y
Dichotomius subaeneus	175	1		176	Y
Dichotomius worontzowi		1		1	Y
Eurysternus atrosericus	66	30	1	97	
Eurysternus balachowskyi	4	27		31	

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Species	Primary	Secondary	*Eucalyptus*	Total	Measured
Eurysternus caribaeus	89	112	14	215	Y
Eurysternus cayennensis		1		1	Y
Eurysternus cyclops	2			2	
Eurysternus foedus	10	118	2	130	Y
Eurysternus hamaticollis	1			1	Y
Eurysternus hypocrita	52	5		57	Y
Eurysternus strigulatus	67	19		86	
Eurysternus vastiorum	1			1	Y
Eurysternus ventricosus	15	21		36	
Ontherus carinifrons			468	468	Y
Onthophagus aff. *bidentatus*	42	543	13	598	Y
Onthophagus aff. *clypeatus*		1	1	2	Y
Onthophagus aff. *haemathopus*	17	1	3	21	Y
Onthophagus aff. *marginicolis*	1	1		2	Y
Oxysternon durantoni	11			11	Y
Oxysternon festivum	11	147	98	256	Y
Oxysternon silenus		5		5	Y
Phanaeus chalcomelas	2	20		22	Y
Pseudocanthon aff. *xanthurum*			13	13	
Scybalocanthon sp. A			2	2	
Sulcophanaeus faunus	1			1	
Trichillidium sp. A		3	1	4	
Uroxys aff. *besti*		1		1	
Uroxys sp. A	55	1		56	
Uroxys sp. B	5			5	
Uroxys sp. C	26		1	27	
Total	1,468	2,284	1,852	5,604	

Figure C.4. Morphometric variables regressed against 'trait values', taken from the first principle coordinates axis. R^2 values are from linear regressions. Species belonging to the large group are in blue, and small species in red. Open circles are species for which we determined 'spatial scale values'.

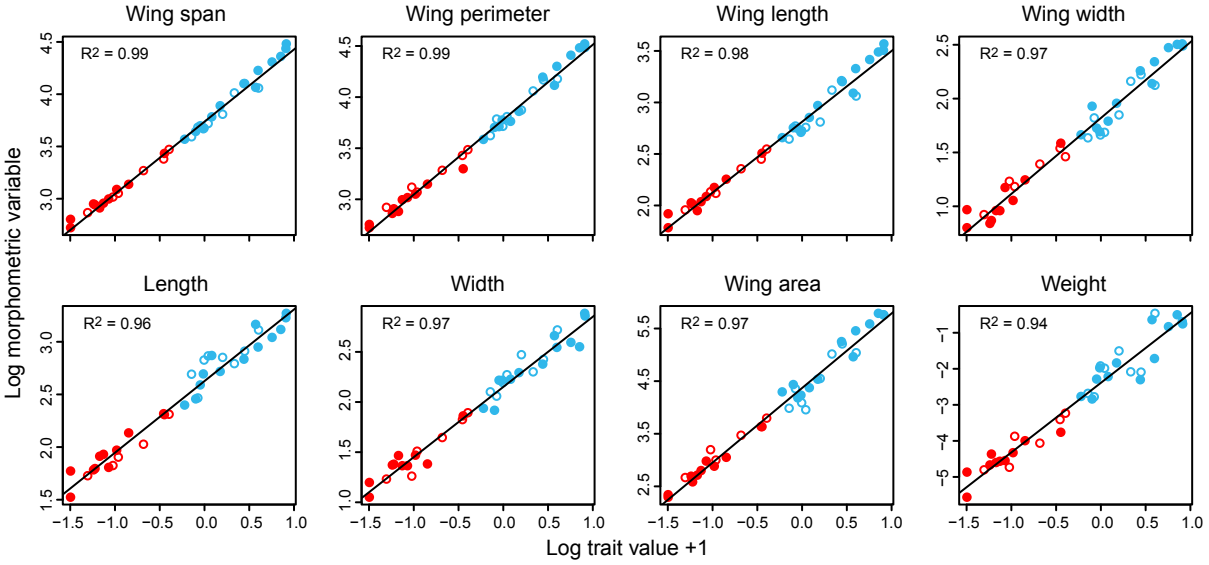
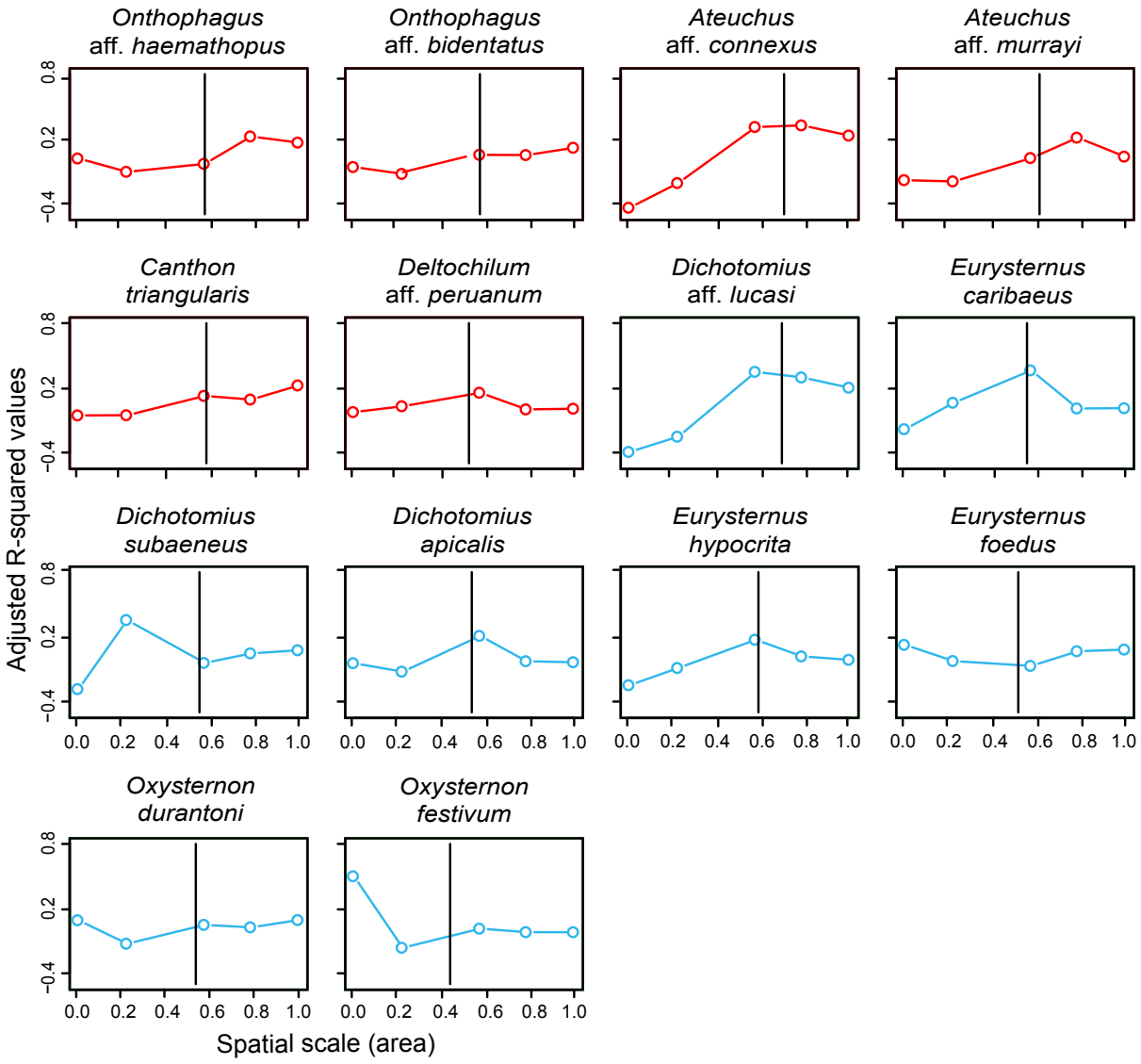


Figure C.5. Adjusted R^2 values for regressions of patterns of species abundance against subsets of DBMEMs. The x-axis represents the total 'area' of eigenvector values for each DBMEM. Vertical lines are the weighted means of the spatial scales determining the patterns of abundance. Species are in ascending order of body weight; the first six species were assigned to the small species group (red), and the last eight species assigned to the large species group (blue).



Appendix D: Supporting information for Chapter 5

Table D.1. Abundance of species at each site

Species	Pri	Sec	Euc	Pri-Sec	Pri-Euc	Total
Ateuchus aff. *candezei*				2	1	3
Ateuchus aff. *connexus*	364	371	9	468	89	1301
Ateuchus aff. *murrayi*	42	317		259	12	630
Ateuchus irinus	8			1	1665	1674
Ateuchus pauki				1	4	5
Ateuchus sp. A	2	3	373	1	7	386
Ateuchus sp. B				1		1
Ateuchus sp. E	1					1
Ateuchus sp. G	1					1
Canthidium aff. *dohrni*					1	1
Canthidium aff. *gerstaeckeri*	3	1		6	3	13
Canthidium aff. *lentum*	4		143			147
Canthidium sp. A	1					1
Canthidium sp. B	3					3
Canthidium sp. D					1	1
Canthidium sp. G	1			8		9
Canthidium sp. H	4			4		8
Canthidium sp. K	2					2
Canthidium sp. L			3			3
Canthidium sp. M	3					3
Canthidium sp. N	1					1
Canthon aff. *acutus*			56			56
Canthon bicolor					73	73
Canthon bimaculatus					1	1
Canthon lituratus			48			48
Canthon quadriguttatus	7				1	8
Canthon scrutator			16		5	21
Canthon simulans		1	545		30	576
Canthon subhyalinus	10	5		11	1	27
Canthon triangularis	58	145	2	84	113	402
Coprophanaeus dardanus		3				3
Coprophanaeus jasius					1	1
Coprophanaeus lancifer			1	1		2
Deltochilum aff. *peruanum*	18	294		143	122	577
Deltochilum aff. *submetallicum*	34	2		16	5	57
Deltochilum carinatum	2					2
Deltochilum icarus	1			15		16
Deltochilum orbiculare	7	2		26		35
Deltochilum sp. A	1			3		4
Deltochilum sp. B					1	1
Dichotomius aff. *lucasi*	114		4		10	128
Dichotomius apicalis	113	5		2	10	130

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Species	Pri	Sec	Euc	Pri-Sec	Pri-Euc	Total
Dichotomius boreus	6		6	27	17	56
Dichotomius carinatus		15				15
Dichotomius imitator					3	3
Dichotomius latilobatus	3	6	29		35	73
Dichotomius mamillatus	1	56		36	27	120
Dichotomius roberti				2		2
Dichotomius subaeneus	175	1		2	1	179
Dichotomius worontzowi		1			29	30
Eurysternus atrosericus	66	30	1	78	33	208
Eurysternus balachowskyi	4	27		24	3	58
Eurysternus caribaeus	89	112	14	92	141	448
Eurysternus cayennensis		1		1		2
Eurysternus cyclops	2			4		6
Eurysternus foedus	10	118	2	47	8	185
Eurysternus hamaticollis	1			1	1	3
Eurysternus hypocrita	52	5		114		171
Eurysternus strigulatus	67	19		50	28	164
Eurysternus vastiorum	1			34	128	163
Eurysternus ventricosus	15	21		14	1	51
Ontherus carinifrons			468			468
Ontherus sulcator					282	282
Onthophagus aff. *bidentatus*	42	543	13	218	417	1233
Onthophagus aff. *clypeatus*		1	1			2
Onthophagus aff. *haemathopus*	17	1	3	23		44
Onthophagus aff. *marginicolis*	1	1			84	86
Oxysternon durantoni	11				1	12
Oxysternon festivum	11	147	98	60	2	318
Oxysternon silenus		5		2	1	8
Phanaeus chalcomelas	2	20		18	12	52
Pseudocanthon aff. *xanthurum*			13			13
Scybalocanthon sp. A			2		7	9
Sulcophanaeus faunus	1			1		2
Trichillidium sp. A		3	1	7	14	25
Uroxys aff. *besti*		1				1
Uroxys sp. A	55	1		15	84	155
Uroxys sp. B	5			5		10
Uroxys sp. C	26		1	30	50	107
Total	1,468	2,284	1,852	1,957	3,565	11,126

Figure D.2. Sample-based species accumulation curves for five sites: primary forest (solid black), secondary forest (solid dark grey), *Eucalyptus* forest (solid light grey), primary-secondary forest edge (dashed black), and primary-*Eucalyptus* forest edge (dashed grey)

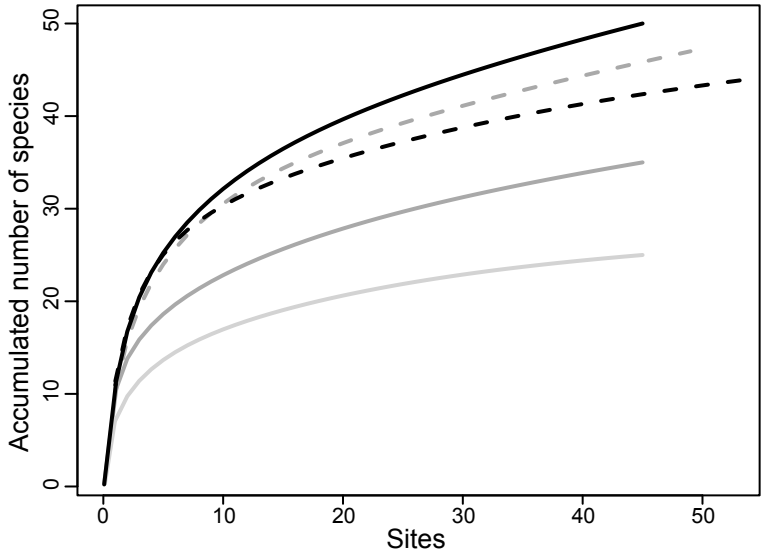


Table D.3. Observed and incidence-based predicted species richness for each of the five study sites

	n	Observed	Jack 1 (se)	Jack 2	Chao (se)	Bootstrap (se)
Primary forest	45	50	64.7 (4.0)	75.3	78.1 (20.9)	56.1 (2.3)
Secondary forest	45	36	46.8 (3.5)	54.5	56.2 (17.4)	40.6 (1.8)
Eucalyptus	45	25	29.9 (2.2)	31.9	29.2 (4.9)	27.4 (1.3)
Primary-Secondary	54	44	52.8 (3.3)	56.8	52.1 (7.1)	48.1 (1.9)
Primary-Eucalyptus	49	47	60.7 (4.6)	72.3	96 (44)	52.5 (2.4)

Figure D.4. Richness matrices across the primary-*Eucalyptus* forest edge. (a) sampling effort based rarefied species richness. (b) Mean community evenness measured through Shannon diversity, (c) mean proportion of singletons and (d) mean abundance per trap night between all traps with each distance category. Error bars are ± standard error. Distance categories of -10^2 and $10^{2.5}$ have been excluded as they were atypical of the habitat.

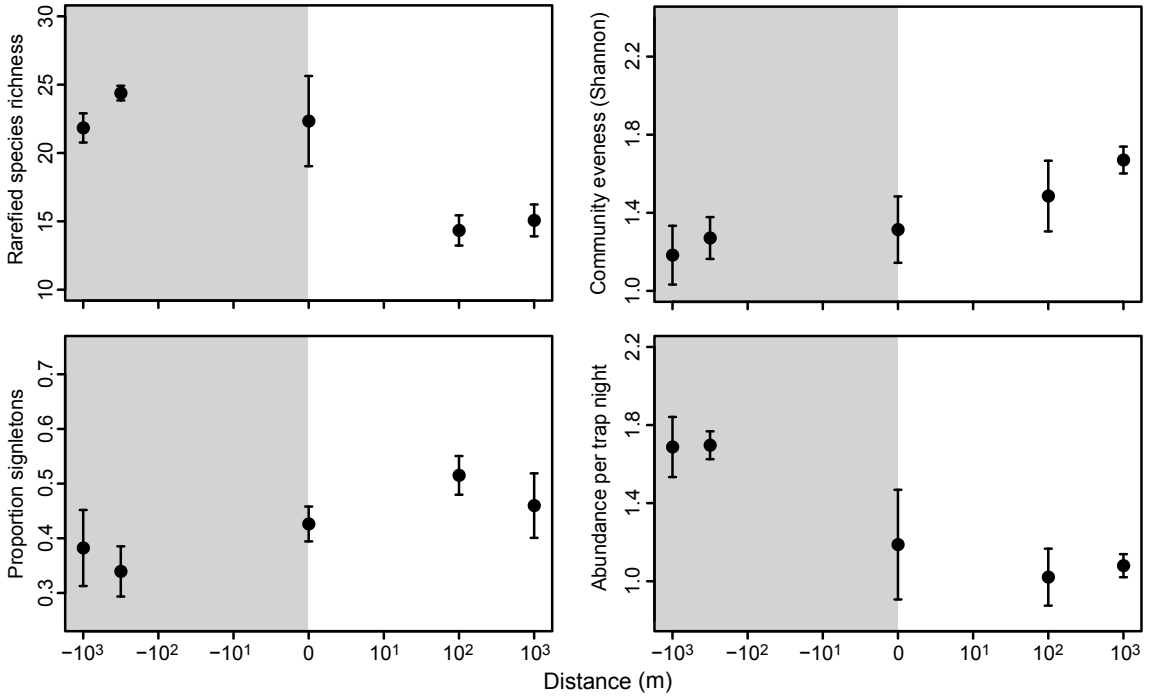
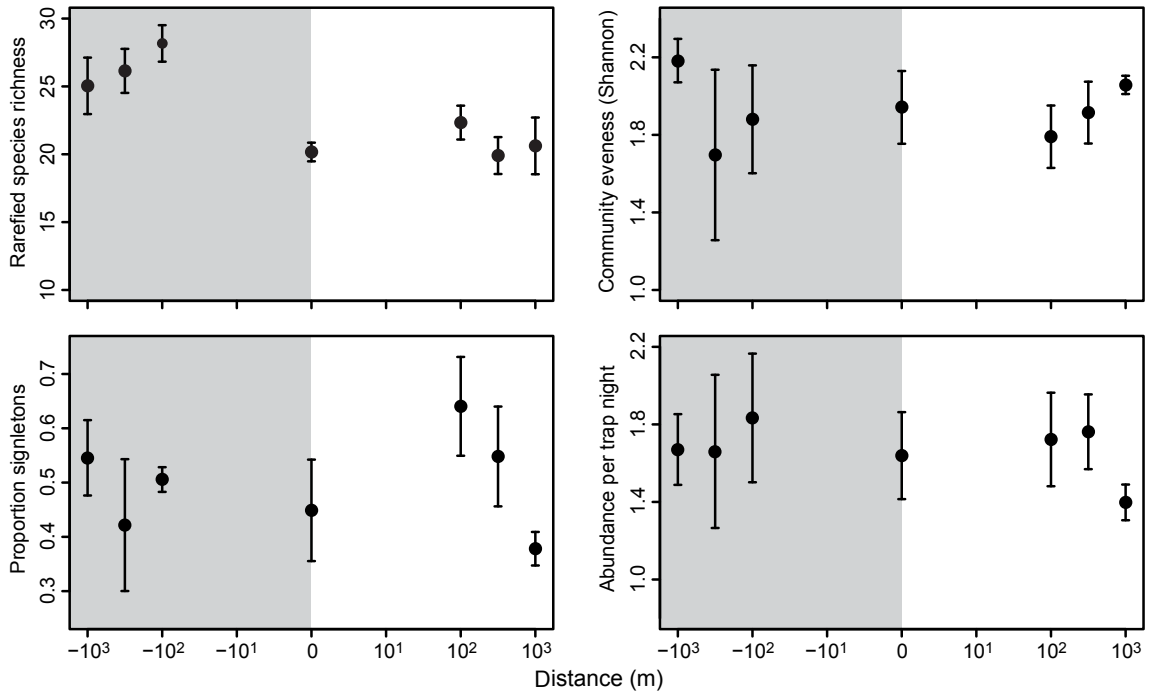


Figure D.5. Richness matrices across the primary-secondary forest edge.



Appendix E: Supporting information for Chapter 6

Figure E.1. Mean ± se for four vegetation characteristics measured at seven distances across the forest edge in the primary forest (negative values, shaded grey) and the matrix habitat (positive values) for two edges, one of primary forest bordering secondary forest (blue) and the other of primary forest bordering *Eucalyptus* (red). Open circles are the estimates from control sites far from habitat edges (>0.95 km).

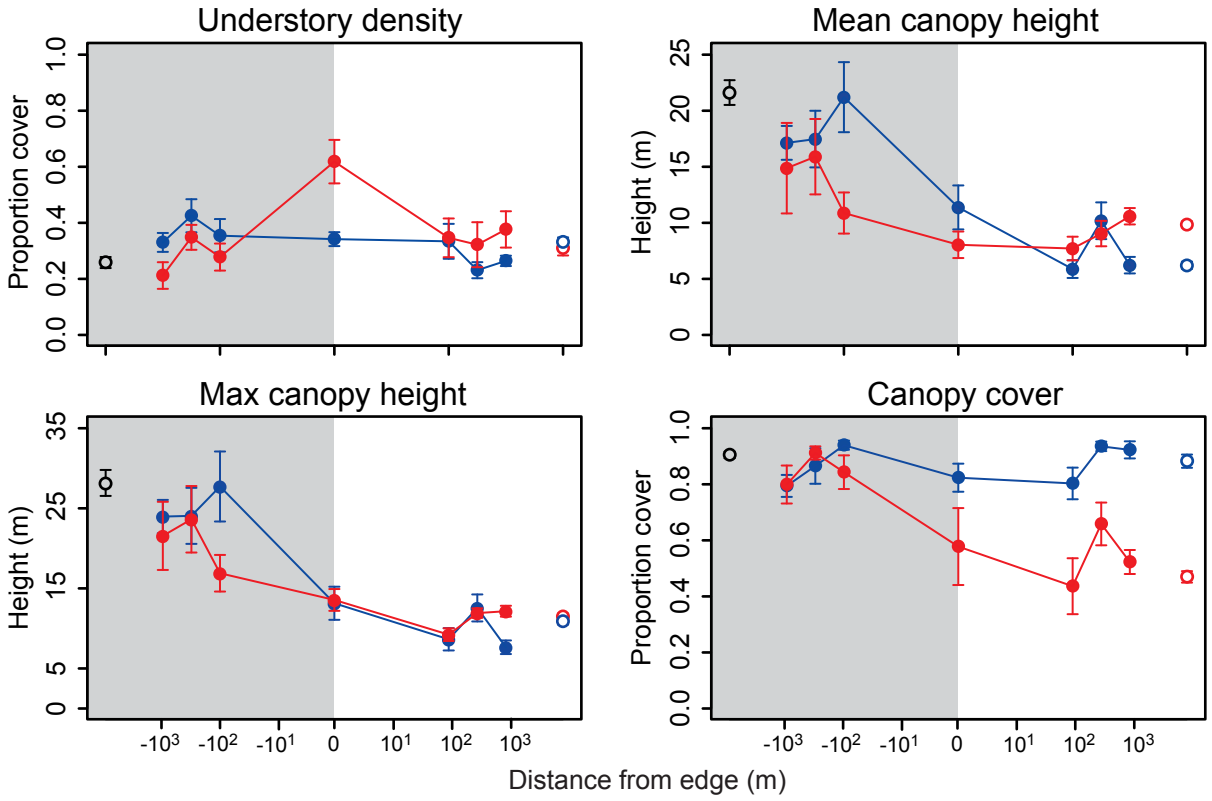
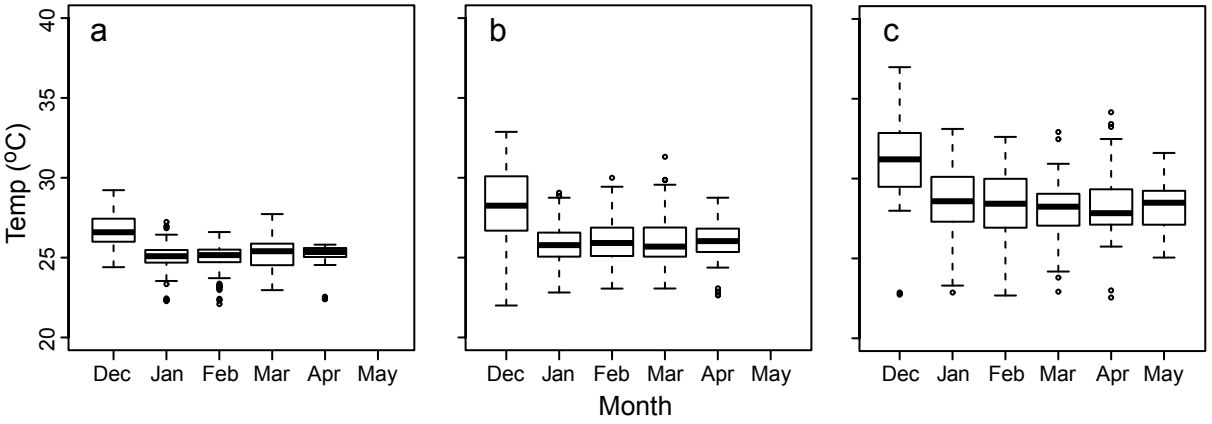


Figure E.2. Boxplots of midday temperatures at ∼30 cm above ground-level in a) primary, b) secondary, and c) *Eucalyptus* forest. Boxes are the first to third quartiles and horizontal lines are median values Whiskers extend up to 1.5 times the interquartile range and points outside 1.5 times the interquartile range (open circles) indicate outliers.



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